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ECOLOGICAL CONTROL OF HYBRIDIZATION IN *QUERCUS*: A FACTOR IN THE MECHANISM OF EVOLUTION [1, 2]

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INTRODUCTION

An understanding of genetic plant geography is impossible without an understanding of the ecological filters through which genotypes of heterogeneous populations are sifted and various segregated. If genetic elements of ecologically diverse species are involved, the pattern of distribution and survival of individuals is strongly dependent upon the occurrence of certain elements of the habitat. This dependence has been clearly shown by Camp (1942), Camp and Gilly (1943), and by Anderson (1948) to be responsible for the occurrence of certain intermediate individuals only in habitats intermediate in character between those to which their respective parent species are adapted. Anderson regarded the operation of this influence as responsible for the rarity of hybrids between some pairs of closely related species with overlapping ranges. Camp credited such ecological restriction of gene exchange with responsibility for continued distinctness of interfertile species of *Vaccinium* with overlapping ranges.

The purpose of this paper is to describe some clear cases of control by habitat factors of hybrid survival in *Quercus*, to point out some equally clear exceptions to the operation of the influence, and to describe the role of the phenomenon in particular cases of evolution.

The habitat factors exercising control are related to soil type and moisture supply (precipitation effectiveness). Characteristics of the habitat are not often determined by soil alone. Although the effect of some soil constituents may control plant survival in spite of varying climatic conditions, those soil factors relating to moisture supply and aeration are functions of climatic elements (precipitation and temperature or evaporation) playing

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upon the framework provided by soil composition and structure. Edaphic differences of habitats, then, are frequently differences in the effectiveness of climate as permitted to operate by soil conditions.

There exists no exact physiological definition of the mechanism whereby arenophilous plant species are confined to sand while non-arenophilous species are restricted from sand. Similarly, the selective action of limestone in determining the distribution of calciphilous species is subject to no general definition applicable to all species. Soil differences comprise a complex of factors at best. Although we cannot at this time define or measure the responsible factors more accurately than by naming the complexes "sand," "limestone," "clay," etc., we can know these complexes well by their end results. A given species either tolerates a given soil or it does not. Some *Quercus* species are especially highly specific in their edaphic requirements.

Longitudinal variation in the climatic factors of the area under consideration takes principally the form of a seasonally and annually fluctuating rainfall gradient devoid of any sharp breaks. As this gradient falls to the west, certain eastern species disappear with corresponding gradualness. There probably exists no exact or definable value responsible for this disappearance, particularly since rainfall effectiveness is determined in part by soil characteristics.

Although the environmental complex is clearly comprised of an interrelationship between climatic and edaphic factors, it is often possible to assign to one or the other of these the rank of limiting factor. For instance, where soil is homogeneous over a wide longitudinal range and a species gradually diminishes in abundance as rainfall values decrease, drought is clearly limiting the farther westward spread of that species. Or, where soil varies sharply in a small area of homogeneous climate, the strict limitation of a species to one soil type is clearly dependent upon the nature of that edaphic complex. The purposes of this paper are thus served adequately by the qualitative definition of factors of the habitat.

The species of *Quercus* are notoriously variable in trivial characters. This variability has given rise to the belief that the oak species hybridize freely. It is quite evident from a study of herbarium specimens, however, that the bulk of the claims of hybridity are based upon trivial variations of the sort one may encounter in a relatively pure population of a single species. A few reputed hybrids, however, do show admixtures of the fundamental characters of their parent species, thus justifying the claim of interspecific hybrid origin. I have in the past expressed opposition to the indiscriminate naming of hybrid oaks (Muller, 1942a, p. 478; 1942b, p. 5) on the grounds that most such designations are unfounded. A clearly demonstrated case of hybridity, on the other hand (e.g., Epling, 1947, and Stebbins, Matzke, and Epling, 1947), is to be welcomed as an aid to understanding the present status as well as perhaps the origin of certain species.

Anemophilous plants, such as the oaks, blooming during the same period are provided with ample opportunity for exchange of pollen. Since most species of *Quercus* growing within a given zone bloom at about the same time, the oaks are subject to no effective pollination barriers amongst contiguous species. The production in *Quercus* of a hybrid plant then depends upon (1) genetic compatibility of the parents, (2) contiguity of range of the parents, and (3) suitable site conditions for the growth of the progeny. Most closely related pairs of *Quercus* species are compatible, but there are many pairs of fairly closely related species between which no intermediates of hybrid origin have been satisfactorily demonstrated. Perhaps some of these remain only to be discovered and certainly some are nonexistent solely because of geographic or ecological barriers between

the possible parents. This, however, is not the case in one group of intermingled species on the Edwards Plateau of Texas.

The rough limestone slopes of the Edwards Plateau bear dense thickets of shrubby or small-tree species of white oaks in great abundance. One of the most extensive of these is *Q. sinuata* var. *breviloba* (Torr.) C. H. Mull. This variety is coextensive in high degree with *Q. virginiana* var. *fusiformis* (Small) Sarg. and to a lesser extent with *Q. Laceyi* Small, *Q. pungens* var. *Vaseyana* (Buckl.) C. H. Mull., and *Q. Mohriana* Buckl. Since all these species and varieties are obligate inhabitants of limestone, they occur closely intermingled wherever their ranges coincide. They are, then, both geographically and ecologically well suited to free hybridization. However, the failure of any intermediate forms to appear in the abundant herbarium collections of these species and in their intensive and extensive study in the field is conclusive evidence that hybridization, if it occurs at all, is very rare.

The five entities named are closely related to one another so that genetic compatibility would be expected. In fact, three of their number have been known to hybridize with a single additional species (*Q. stellata* Wang.). The entities are not only distinct morphologically, but they exhibit easily recognizable characters that would serve to call attention to any case of genetic intermixture amongst them. The failure of such intermixture to appear is explicable, then, only in terms of genetic barriers as yet not demonstrated.

Remotely related oaks, on the other hand, apparently do not hybridize. Trelease (1924, p. 12) stated that he knew of no case of hybridity except between species of the same subgenus. This appears to be correct.

Although many pairs of species have overlapping ranges, some are effectively isolated. Contiguity or overlapping of range may be controlled by climatic as well as edaphic factors. Reduced precipitation limits the westward extent of many eastern North American species. However, some species may occupy sandy soil far to the west of the general western limit imposed upon them by rainfall levels. Some species of desert regions are limited to montane situations of high elevation and resulting high precipitation and low temperature and evaporation. Several species exhibit strict confinement to a single type of substratum. Thus some are completely confined to limestone outcrops with thin layers of soil, some to igneous outcrops, some to sand, and some to gravelly clays, sometimes overlaid by shallow sand. Should two such types fail to approach each other, the species associated with these soils remain effectively isolated.

Lack of suitable site conditions for hybrid progeny constitutes a barrier to effective hybridization in many cases. When the edaphic requirements of the parents are markedly at variance with each other, it appears that a site suitable for a hybrid is often produced by a mixing of soil types at their line of contact. If the parental requirements consist of significantly different climatic conditions, contiguity of range is impossible and the suitable intermediate climatic conditions would lie beyond the normal distance of acorn dispersal.

A few selected pairs of parent types that have been studied in the field throughout their ranges of distribution will serve to illustrate the extent to which these influences are operative in determining the facts of hybridization in *Quercus*. Not all of the apparent cases of hybridity are clearly explicable upon ecological grounds, and some very clear exceptions are discussed.

The hybrid forms here cited and their respective parent species have all been treated taxonomically and illustrated photographically elsewhere (Muller, 1951b). In that treatment all pertinent herbarium specimens are cited and the taxonomic characters and other forms of evidence upon which the opinions of hybridity are

based have been described. In a few illustrative cases these characters are again described here for the sake of clarity. In the course of the field studies no counts were preserved, but the number of living plants studied many times exceeds that of herbarium specimens taken. It would be difficult to estimate the number of individuals examined in each case of hybridity discussed. In the instance of *Quercus Mohriana* and *Quercus grisea* the combined field and herbarium studies involved several thousand individuals, at least a thousand of these occurring in areas of effective hybridization and including hundreds of hybrids. In the study of *Quercus Havardi* and *Quercus stellata* an even greater number of individuals was employed. In some cases, e.g., *Quercus incana* and *Quercus marilandica*, small populations numbering less than a hundred parents and intermediates were studied. The field studies involved literally weeks of walking from bush to bush examining each for evidence of the presence of extraspecific genetic characters.

The very obvious nature of hybrid swarms in *Quercus* eliminates the necessity of statistical approaches, progeny tests, and similar proofs of hybridity. Cytological analyses, while they frequently are invaluable aids to such a study as this, are unfortunately inapplicable to *Quercus* in which no aberrations in chromosome number and morphology are known.

Edaphic Restriction of Hybridization

Two species of similar climatic requirements and occupying the same general area may differ markedly in their soil requirements. Such differences may serve to keep the species sufficiently isolated to prevent hybridization if the proper soil types do not occur within pollination range. Should the types meet, effective hybridization will depend upon the development of intermediate sites suited to the requirements of the hybrid progeny. In the following illustrative cases several degrees of edaphic control of hybrid survival are described.

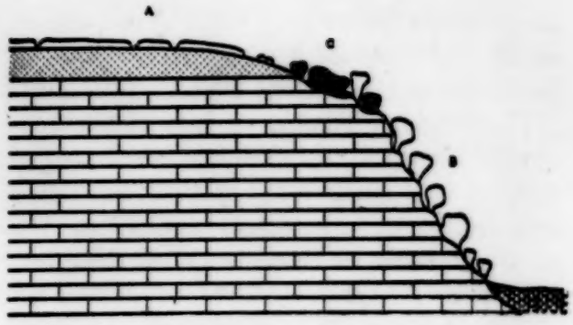

Fig. 1. Profile section of a contact between *Quercus Havardi* and *Q. Mohriana:* A, pure *Q. Havardi* on deep sand; B, pure *Q. Mohriana* on exposed limestone; C, intermediates of hybrid origin on a mixture of sand and limestone fragments.

Quercus Mohriana and Quercus Havardi

Quercus Mohriana Buckl. ranges northward from Coahuila, Mexico, into the Trans-Pecos region of Texas and thence eastward onto the Edwards Plateau and northward along the "breaks" of the plains into the Panhandle of Texas. Throughout this range it is invariably found upon limestone (or dolomitic limestone) or in shallow soils overlying limestone. Its restriction is perhaps more strict than that of most "obligate" species. Its extension into the Great Plains region is entirely dependent upon Cretaceous outcrops or upon the exposure of limestone strata of Permian age resulting from the erosion of the plains by drainage systems.

Quercus Havardi Rydb. ranges from southeastern New Mexico eastward across the southern Great Plains to southwestern Oklahoma. It is strictly confined to sand belts of considerable depth and high degree of coarseness. Where erosion happens to coincide with such a sand area, *Q. Havardi* approaches closely the exposed limestone ledges harboring *Q. Mohriana.* (See fig. 1.)

Impressive examples of such contacts may be seen seven miles west of Dickens, Dickens County, Texas, and two miles south of Eppler, Garza County, Texas.

Several other contiguous populations were also studied.

The interchange of pollen permitted by these contacts produces progeny intermediate in form between the two species. These individuals exhibit a high degree of morphological variability suggestive of segregation incidental to backcrossing. In some instances the hybrid plants are nearly identical with one or the other parent while others are approximately intermediate in form. The population thus formed shows a strong tendency toward differential distribution. As shown in figure 1, *Q. Havardi* occurs in nearly pure stand on deep sand (at A) while *Q. Mohriana* is similarly confined to exposed limestone (at B). The brow of the bluff is composed of a mixture of sand and limestone fragments (at C). This intermediate habitat is occupied almost exclusively by the hybrid individuals. In no instance were strongly intermediate individuals found outside the intermediate habitat. Very dilute hybrids of *Q. Havardi* with a few morphological characters of *Q. Mohriana* occasionally occur in habitat A with pure *Q. Havardi*. Similarly, very dilute hybrids of *Q. Mohriana* with few characters of *Q. Havardi* appear with pure *Q. Mohriana* in habitat B. There are thus strong correlations between (1) intermediacy of the habitat and intermediacy of the hybrids present and (2) degree of purity of the habitat and degree of purity of the parent species occurring there.

The differential distribution reflected by these correlations indicates a parallel between morphological and physiological characters. Morphologically pure individuals are apparently genetically pure (that is, not interspecific hybrids) and are physiologically pure; these grow in habitats ideally suited to the species to which they belong. Morphologically intermediate individuals are obviously of hybrid origin and seem to be physiologically intermediate; these grow only in intermediate habitats. Only very dilute hybrids (as indicated by their slight morphological differentiation) can grow with the parent species in their respective ideal habitats.

This limitation imposes a slow rate of gene exchange which must necessarily be of limited effectiveness in changing the essential nature of any sizable population of either species. Yet, its importance is indicated by the fact that there exist incipient minor but perceptible morphological differences between the populations of *Q. Mohriana* in Coahuila and Trans-Pecos Texas and those of the plains where the contacts with *Q. Havardi* occur. However, much more rapid rate of gene flow can be demonstrated in other cases.

Quercus Mohriana and Quercus grisea

Quercus grisea Liebm. is an almost obligate inhabitant of the igneous outcrops of Trans-Pecos Texas, New Mexico, Arizona, and Chihuahua, Mexico, but may sometimes occur on adjacent dolomitic limestones of Permian age, notably in the Guadalupe Mountains, the Diablo Plateau, and the Glass Mountains of Trans-Pecos Texas. However, the Cretaceous limestones of eastern Trans-Pecos Texas are completely free of the species.

It was noted above that *Q. Mohriana* is confined to limestone outcrops. Although its best development occurs on Cretaceous limestones of the Comanche series, the species is also vigorous on several Permian limestones and dolomites.

The nature of the contact between *Q. grisea* and *Q. Mohriana* is two-fold. Where Cretaceous limestones and igneous rock are contiguous, the two species approach the line of contact in nearly pure form. Intermediates between the species are confined chiefly to a narrow zone of mixed limestone and igneous rock along the line of contact. Such a case may be observed about twelve miles east of Alpine, Brewster County, Texas, at the northwest end of the Del Norte Mountains (Cretaceous limestone) where they come in contact with outlying basaltic elements of the igneous Davis Mountains system. Immediately across the narrow

valley, however, and less than two miles distant, intricately intermixed populations of *Q. grisea, Q. Mohriana,* and their intermediates occur on the southwesterly foothills of the Glass Mountains which are composed of Permian dolomites. These populations have no easily discernible pattern of distribution. However, more distant from the igneous Davis Mountains, these dolomites bear only *Q. Mohriana* with a slight admixture of *Q. grisea* genes.

In this general area gene flow from *Q. grisea* into the *Q. Mohriana* population is occurring at a seemingly inconsequential rate. Reciprocal flow of *Q. Mohriana* into *Q. grisea* populations appears (from morphological evidence) not to take place at all. The igneous rock habitat of *Q. grisea* populations seems inhospitable to any genotype sufficiently related to *Q. Mohriana* to exhibit morphological evidence of such a relationship.

A quite different form of contact between *Q. grisea* and *Q. Mohriana* occurs on the dolomitic outcrops of the Diablo Plateau in eastern Hudspeth and western Culberson Counties. Here the substratum appears to be almost equally fitted for both species, although *Q. Mohriana* is considerably more abundant than *Q. grisea.* Free hybridization results from this broad intermingling and the number of intermediates is at least as great as the number of pure *Q. grisea* individuals although not approaching the abundance of pure *Q. Mohriana.* The absence of any adjacent reservoir of *Q. grisea* places a distinct limit upon the potential degree of gene flow unless some future return of moist climatic conditions permits a wholesale migration of that species down from the mesic habitats of the igneous Davis Mountains.

A somewhat similar contact between the two species occurs in the Guadalupe Mountains of northwestern Culberson County and adjacent northeastern Hudspeth County, Texas. Here, however, the ratio of relative abundance of the two parent species is reversed. The lofty mountains provide ample habitats for a large population of *Q. grisea.* The number of "pure" *Q. Mohriana* individuals, on the other hand, is far exceeded by the number of intermediates between the two species. Although *Q. Mohriana* has left a distinct imprint upon the *Q. grisea* population, its own persistence in this area is a doubtful matter.

Quercus Mohriana and Quercus stellata

The intrusion of *Q. Mohriana* into the plains region along the exposures of Cretaceous limestones or Permian dolomites brings it into contact with *Q. stellata* Wang., a species with which it hybridizes infrequently. *Quercus stellata* occupies extensive areas of gravel, clay and gravel mixtures, and sandy clay extending westward from Central Texas. These deposits are of more recent age than the Cretaceous, some of them being even of Pleistocene age. Where some of these diverse strata lie upon Cretaceous limestones, erosion has exposed limestone ledges which are occupied by *Q. Mohriana.* The close proximity of *Q. stellata* on suitable overlying gravel beds permits cross pollination. Such zones of contact were observed one and one-half miles southwest of Ovalo, Taylor County, and eight miles south of Sweetwater, Nolan County, Texas, on sandy gravel slopes overlying limestone and on eroded limestone banks.

The survival of intermediate forms seems to be very rare, for only a few apparent hybrids were encountered in the several areas of contact. These intermediates were confined to the zone of mixture of sand, gravel, or clay and limestone fragments. It would appear that the requirements of the two parent species are too diverse and that the absence of very extensive intermediate habitats also drastically restricts the areas in which intermediate individuals might become established. However, it is also possible that some degree of incompati-

bility contributes to the infrequency of hybrids between these species.

Quercus incana and Quercus marilandica

The peculiar pattern of outcropping of geologic strata across Central Texas is responsible for the degree of isolation of a pair of species of the black oak subgenus. One of these is *Q. incana* Bartr. (*Q. cinerea* Michx.) which is strictly confined to areas of deep sand that extend across Texas from the northeast. The species ranges eastward to Florida and Virginia on similar sand beds. Adjacent to these sands occur outcrops of mixed gravel and clay on which *Q. marilandica* Muench. is abundant. This species ranges from the Edwards Plateau and coastal Texas eastward to the Atlantic and northward to Kansas and New York. *Quercus marilandica* can occupy sand areas only if they are heavily impregnated with clay or shallowly overlie clay. Because each species is strictly inhibited by the ideal site of the other, their points of contact are limited to those situations in which such sites approach each other. The two species were studied at the site of such a contact on sandy clay hills seven miles south of Woodville, Tyler County, Texas.

Wherever the two species intermingle some intermediates of hybrid origin are to be expected. The intermediates show evidence of their hybrid origin by various combinations of the characters of the parents. Amongst these the fulvous-tomentose buds, the similarly fulvous and loosely appressed cup scales, and the toothed or clavately lobed and aristate-tipped leaves of *Q. marilandica* are outstanding when combined variously with the nearly glabrous or gray-villous buds, gray and closely appressed cup scales, and entire oblong leaves with gray-tomentose lower surfaces characteristic of *Q. incana*. The degree of heterogeneity of the intermediates indicates that some backcrosses have occurred. These hybrids, as in the case of earlier examples, occur only on sites intermediate in character between those of the parents. Such mixture of substratal elements occurs quite commonly between the sand and clay zones so that sites favorable to hybrids are common. The number of intermediates, however, is not very large and apparently does not indicate any highly significant gene flow.

Quercus Margaretta and Quercus stellata

Quercus Margaretta Ashe is a shrubby or small-tree species ranging from central and northern Texas eastward to Florida and Virginia. The distribution of *Q. Margaretta* is determined by the extent within its general range of beds of deep sand, of which it is an obligate inhabitant. Such sands are provided by outcrops of Eocene age (Sellards, Adkins, and Plummer, 1932, p. 530 *et seq.*) running diagonally across Texas from southwest to northeast and by additional strips in southeastern and northcentral Texas of later and earlier ages, respectively. These habitats are represented eastward along the Gulf and Atlantic Coastal Plains by similar sands of comparable ages.

Adjacent to the sand zones and sometimes intermixed with them are clay and gravel beds of various Tertiary or early Pleistocene ages on which *Q. stellata* occurs. The proximity of the two substratal types therefore brings the two species into close contact. That they do not freely hybridize and thus merge can be ascribed only to the fact that neither species is tolerant of the soil conditions that favor the other. Thus beds of deep sand bear pure stands of *Q. Margaretta* in relatively pure form, while beds of gravel and clay sometimes overlaid by shallow sand bear pure stands of *Q. stellata* in equally undiluted condition. Sites in which the substratal types are mixed and therefore ecologically intermediate frequently bear plants intermediate between the two species and obviously of hybrid origin. The evidence supports the conclusions that in this case genetic incompatibility does not exist as an effective barrier to hybridization and that ecologi-

cal selection acts as a control of the process apparently to a degree similar to that described for *Q. Havardi* and *Q. Mohriana* hybrids. However, in the present instance the intermediate habitats are more common and of greater area with the consequence that the number of recorded cases of hybridization is much greater. Analyses of hybrid populations were made at widely scattered points through Texas.

Climatic Restriction of Hybridization

Plant migrations have undoubtedly played and are playing a part in determining the incidence of hybridization. In several cases of recent hybridization in *Quercus* it appears that climate is the restrictive factor, operating, however, through the strong edaphic influence of a deep sand substratum.

It is an ecological truism of paradoxical nature that in a region of high rainfall sand is the driest possible soil type, while in a region of low rainfall sand is the moistest possible soil type. For this reason relict species in an arid region are found on sand, or, to express it in another way, in a dry region plants with moderately high water requirements can persist only on sand. This has resulted in the persistence in the plains region of arenophilous species far to the west of their normal rainfall requirements.

Quercus Havardi and Quercus stellata

Quercus Havardi (as describe above) is confined to the sand belts of the southern Great Plains, from southeastern New Mexico to southwestern Oklahoma. It grows rapidly by spreading rhizomes when relieved from competition of the grass cover of its native sand hills (e.g., removal of the competing grasses by overgrazing). From these rhizomes it produces usually simple shoots one to three feet in height which form dense thickets ten to thirty feet in diameter. The limits of each clone can be recognized by minor variation in leaf size, form, color, pubescence, etc.

The plants within a particular locality are usually uniform in height, but clones may be found which stand eight or ten feet in height and tower above their surrounding neighbors. Such clones vary from typical *Q. Havardi* in such a way as to indicate introgression from *Q. stellata,* a tree species. The short, white pubescence of the lower leaf surface characteristic of *Q. Havardi* may be replaced by obviously spreading pubescence of gray or tan hairs of *Q. stellata;* the normally oblong, entire or toothed leaf may be much broader and obscurely or markedly round-lobed; the rather large fruit may be only half as large and the usually deep, fringed cups with attenuately narrowed scales may be more shallow, lacking a fringe, and the scales not markedly narrowed. Most of the characters except height vary quite independently of one another. Examination of thousands of clones, especially in areas with a high percentage of variants, failed to reveal a single obvious leaf or fruit variant not associated with increased height.

As one follows the range of *Q. Havardi* from west to east, the first variant clones are encountered in the extreme western counties of the Panhandle of Texas in an area characterized by an average annual precipitation of about 15 inches (U.S. D.A., 1942). As one continues eastward and somewhat northward the taller clones increase in number and in similarity to *Q. stellata.* Such increases are particularly apparent in the 22 inch annual precipitation zone in Fisher County, Texas, where the range of *Q. Havardi* is approached from the south by typical *Q. stellata.* In Wheeler County, Texas, and in adjacent western Oklahoma similar increases in frequency and intensity of variation occur. In this area, with an average annual precipitation of 24 inches or more, *Q. Havardi* comes into actual contact with scattered local outposts of *Q. stellata* ranging from the east but no

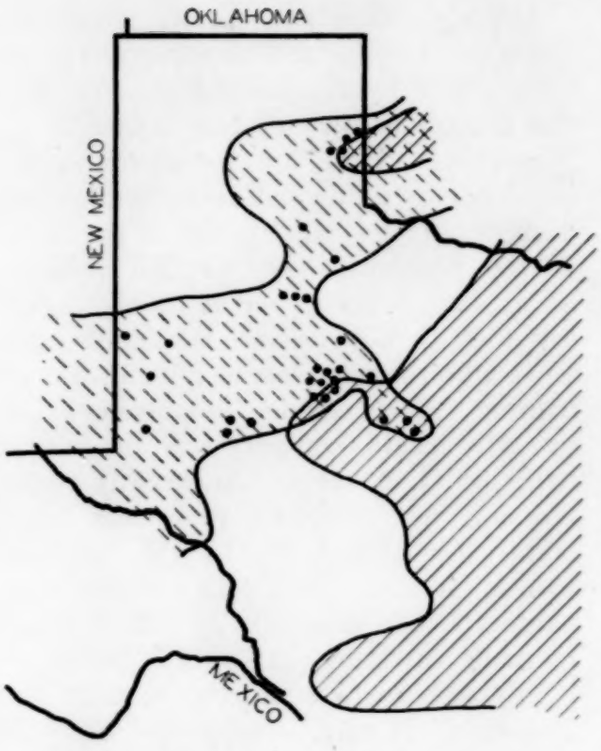

FIG. 2. The contacts between *Quercus Havardi* (broken lines) and *Q. stellata* (solid lines). Sites of known hybrids are indicated by large black dots.

very extensive overlapping of ranges occurs. (See fig. 2.)

During the period of anthesis the strong winds are westerly and sustained. It is not reasonable to assume that *Q. stellata* pollen could have been blown from the present western extremity of the range of that species and resulted in the observed hybrid individuals one hundred and fifty miles to the west. These hybrids are much more likely relics of a relatively ancient series of crosses that occurred during the moist, cool period when *Q. stellata* may have ranged west to the vicinity of the New Mexico boundary on the clay and clay-impregnated sandstones that occur adjacent to several of the zones of deep sand. Subsequent desiccation eliminated from this region all mesophytic species except the arenophiles. All that remains of *Q. stellata* in this area, then, is a series of dilute hybrids with *Q. Havardi,* these possessing enough genectic influence from the latter parent to permit their survival in the sand habitat.

Taxonomists have given several interpretations to the prominently tall hybrids of *Q. Havardi* and *Q. stellata.* Thus Trelease (1924), centering his attention upon the Rocky Mountain region, was impressed by the broad, lobed leaves that suggested to him relationship to the Rocky Mountain oaks (*Q. Gambelii* Nutt). Sargent (1918) came close to the truth (as I see it) when he described the more strikingly variant forms of the east and southeast as varieties of *Q. stellata,* a species with which he had occupied himself at some length throughout its eastward range. Thus the interpretations have been colored by the student's point of view, and the status of the many forms as hybrids could be realized only after field study throughout the ranges of both parents, but especially that of *Q. Havardi.*

The degree to which the easterly populations of *Q. Havardi* have been modified by introgression is difficult to evaluate objectively because of the greater stature of the intermediate individuals which obscure the low, shrubby parent. The persistence of obviously pure *Q. Havardi* over the greater part of the soil area, associated with numerous tall intermediates, would argue fluently for the conclusion that the gene flow has not been of extreme importance. Although the intermediates have the definite advantage in competition by shading of added stature, their failure to drive out the small parent suggests that some other factor is operating to their disadvantage. This might be a physiological character from *Q. stellata* of the sort that restricts that species from deep sand. The great diversity of forms and abundant evidence of backcrossing to *Q. Havardi* is ample proof that several generations have appeared, but that sufficient time has elapsed to permit full expression of the effects of gene flow may be open to question. In so extremely long-lived an organism it is doubtful that death of established clones occurs sufficiently frequently to have permitted the establishment of enough seedlings since the last pluvial period so that

full expression of the hybrid influence is possible. It must be borne in mind that vegetatively reproducing forms of rhizomatous habit are not subject to senescence as are single-stemmed trees (Muller, 1951a). The restriction of *Q. Havardi* from any but very sandy soils distinctly limits the degree to which gene flow into the adjacent *Q. stellata* population can be effective.

Incompatibility

Quercus includes numerous examples of related species of identical habitat requirements that nevertheless fail to hybridize. Such failure is probably the result of incompatibility since neither spatial isolation nor unsuitable seeding sites can be demonstrated.

Quercus Emoryi and Quercus Gravesii

Both *Q. Emoryi* Torr. and *Q. Gravesii* Sudw. inhabit igneous mountain masses of moderately high elevation. *Quercus Emoryi* ranges from Trans-Pecos Texas to Arizona and southward into Chihuahua and Sonora. It is absent from Coahuila. *Quercus Gravesii* occurs abundantly in the Davis, Glass, Chinati, and Chisos Mountains of Trans-Pecos Texas and ranges southward through the Sierra del Carmen of Coahuila. Thus the two species overlap in range only in the mountains of Trans-Pecos Texas. Their habitat requirements are not identical, for *Q. Emoryi* extends onto drier slopes of lower elevation than does *Q. Gravesii*. However, they are intimately mixed over vast areas.

The relationship of these species within the black oak subgenus is relatively remote, for they belong to series both morphologically and geographically diverse from one another. *Quercus Emoryi* is the easternmost representative of the series *Durifoliae* which centers in northwestern Mexico, while *Q. Gravesii* is the westernmost representative of the series *Coccineae* which centers in the Atlantic United States. That they should prove interfertile at all is in itself extraordinary.

Although these two species mingle in scores of canyons in Trans-Pecos Texas, evidences of hybridization appear in only Oak Canyon at low elevation in the Chisos Mountains. Here are found numerous intermediate individuals representing all degrees of resemblance to one or the other of the parents. The biennial fruiting habit, long petioles, and markedly lobed leaves of *Q. Gravesii* are combined variously with the sub-evergreen habit, annual fruiting, short petioles, obscurely lobed or entire leaves, and very stiff and coarse twigs of *Q. Emoryi*. Apparently backcrossing has occurred repeatedly with both parents, and the hybrids are obviously fertile. Inasmuch as the two parents occur together on many other mutually favorable sites, their failure to hybridize elsewhere remains without explanation. It may be suggested that this single recorded instance of hybridization represents the lapse of a state of genetic incompatibility which characterizes the two species elsewhere in their common range.

Quercus hypoleucoides and Quercus Gravesii

A case exactly parallel to the last is also to be seen in *Q. hypoleucoides* A. Camus and *Q. Gravesii*. *Quercus hypoleucoides* ranges from Trans-Pecos Texas westward to Arizona and southward to Sonora, Chihuahua, and Coahuila. Its range overlaps that of *Q. Gravesii* only in Coahuila and in the Davis Mountains of Trans-Pecos Texas. In these localities, however, it occurs thoroughly intermingled with *Q. Gravesii* over vast areas. The site requirements of the two species are strikingly similar and their altitudinal ranges overlap broadly. However, in only one canyon (HO Canyon in the Davis Mountains) does one encounter intermediates of hybrid origin. These combine the long petioles, lobed leaves, and biennial fruiting habit of *Q. Gravesii* with the short petioles, tendency toward entire leaves, impressed-veiny upper leaf surfaces, and white-tomentose lower leaf sur-

faces of *Q. hypoleucoides*. The intermediates are not abundant, but they are apparently fertile, for segregation of characters is obvious in the several individuals studied.

Quercus hypoleucoides is the easternmost member of the series *Hypoleucae* which centers in northwestern Mexico. Its relationship to *Q. Gravesii* is fully as remote as that of *Q. Emoryi*. In both instances these cases of hybridization represent failure of the species to cross effectively as often as geographic and ecological opportunity would have permitted. It appears, then, that phylogenetic remoteness is reflected in a degree of genetic incompatibility that has resulted in decrease in frequency of crossing but not in total elimination of crossing. The obvious fertility of the F_1 as indicated by backcrosses is more puzzling than illuminating.

Speciation in the *Quercus Margaretta* Complex

Scarcely more than a few tentative suggestions have been advanced in explanation of the origin of species in *Quercus*. Yet, students of the genus have freely expressed opinions concerning the origin of the prototypic forms in which the genus was conceived and, from these, of the subgenera as they exist today. Thus Trelease (1924, p. 34) suggested that all the American oaks were derived from an Old World immigrant form corresponding to the living species *Q. chrysolepis* Liebm. whose variants radiated from a center in what is now Arizona and have since given rise to the multiplicity of subgenera, series, and species now inhabiting America. Although this may be entirely true, there may exist some reasonable doubt that the history is quite so simple. In fact, de Candolle (1864, p. 23) suggested a closer relationship between the Californian white oaks and those of western Europe than exists between those of eastern and western America. It could, therefore, be argued that the American prototype was derived from Europe in the form of a white oak, if, indeed it was derived from the eastern hemisphere at all.

It could as well be argued that the genus arose in the western hemisphere where the white oak, intermediate oak, and black oak subgenera diverged and that the white oak subgenus alone bridged the connection across the Aleutians to Asia. This would more nearly conform to the very real relationships demonstrable between the tree species of white oaks in California and those of Western Europe and between the shrubby species of California and those of eastern Asia. Also, the presence of one species of *Lithocarpus* in California, while that genus shows great development in southeastern Asia, would thus reflect a similar route of migration, perhaps traversed in reverse.

It would seem that the broader questions of origin might much better be answered in the light of more detailed knowledge of more recent origins of specific groups. It is toward that end that this study is offered. If the relatively immediate origins of all species in the genus were known even as inexactly as the general reconstruction herein proposed for a few, the origin of higher categories might be sought in morphological and fossil evidence with much greater assurance, if, in fact, such remote developments can be determined.

Speciation in *Quercus* has involved diverse processes embracing geographic isolation, paleo-ecology, contemporary ecology, and hybridization. The relationship of hybridization to ecological control of distribution is discussed critically above and the principle will be applied in the following discussion.

Four species have been chosen for analysis all of which I have studied in the field in some detail while engaged in reviewing the oak flora of Texas. They are referred to the post oak series, *Stellatae*, and to the Rocky Mountain white oak series, *Gambeliae*, both belonging to the white oak subgenus, *Lepidobalanus*.

The Origins of Quercus Margaretta and Quercus Drummondii

The prototype from which *Q. Margaretta* clearly is derived is *Q. Gambelii* Nutt., a species of the Rocky Mountain and Great Basin Regions. The demonstrated genetic compatibility of *Q. Margaretta* with *Q. stellata* is responsible for the differentiation of *Q. Drummondii* Liebm. The history of these derivations is one of paleoecology.

An examination of the present ranges and ecological requirements of these species reveals significant differences. *Quercus stellata* ranges from its present western extremity in west-central Texas eastward to Florida and northward to Kansas and Massachusetts. It is confined to gravelly or sandy clay soils throughout this range. *Quercus Margaretta* ranges on deep sands over the same general area but no farther northward than Oklahoma and southern Virginia. The range of *Q. Gambelii* extends from the mountains of Trans-Pecos Texas northward along the Rocky Mountains into Colorado and Wyoming, westward to Arizona and Utah, and southward to Coahuila and western Chihuahua. It is usually confined to moderate elevations corresponding roughly to the lower and middle yellow pine zone, although it may extend to much lower elevations in favorably moist situations. *Quercus Drummondii* replaces *Q. Margaretta* at the western extremity of its range. The much more extensive ranges of *Q. stellata* and *Q. Gambelii* are in keeping with their roles as representatives of the prototypes from which *Q. Margaretta* and *Q. Drummondii* were derived. *Quercus Gambelii,* at least, must have been widespread long before desiccation incised its range and caused the present isolation of its many widely scattered populations.

Geologic evidences of several kinds indicate a period of increased precipitation at the close of the Tertiary and in the Pleistocene. The extensive deposits of waterworn coarse gravels now occupied by *Q. stellata* required high rainfall to account for their transportation to the flood plains of rivers where they were laid down (Sellards, Adkins, and Plummer, l.c., pp. 784, 785). During such a pluvial period the spread of *Q. Gambelii* stock eastward over the southern plains area would have been possible. Simultaneously, the westward extension of *Q. stellata* from an eastern center could have occurred. The two prototypes would have met either on the plains or to the east of that area. The ecological circumstance of apparent close agreement between the habitat requirements of *Q. Gambelii* stock and the edaphic qualities of the deep sand strips provided a migration route to the Atlantic along the Gulf Coastal Plain. This also provided a buffer against free hybridization with adjacent *Q. stellata* (described above under "Edaphic Restriction of Hybridization") so that gene flow progressed at a retarded rate.

The subsequent desiccation of the entire region has resulted in recession of the prototypes from the southern Great Plains and consequent isolation of the Gulf Coast populations from those of the Rocky Mountains. Local recessions under conditions of reduced rainfall would have removed both species from the less suitable soil types upon which high rainfall had permitted them to become established. The eastward recession of *Q. stellata* is clearly shown by the occurrence of hybrids with *Q. Havardi* far beyond the present western limit of *Q. stellata* as described above. Continued current recession is indicated by the numerous relict stands of *Q. stellata* at its western extremities where seedlings and young trees are extremely rare.

The movement of *Q. Gambelii* eastward would have required a period of time so that hybridization with *Q. stellata* might have begun in Central Texas earlier than in the Atlantic region. Thus the westernmost populations still living would be expected to show a greater amount of introgression than those of the east. This has, in fact, resulted in introgression

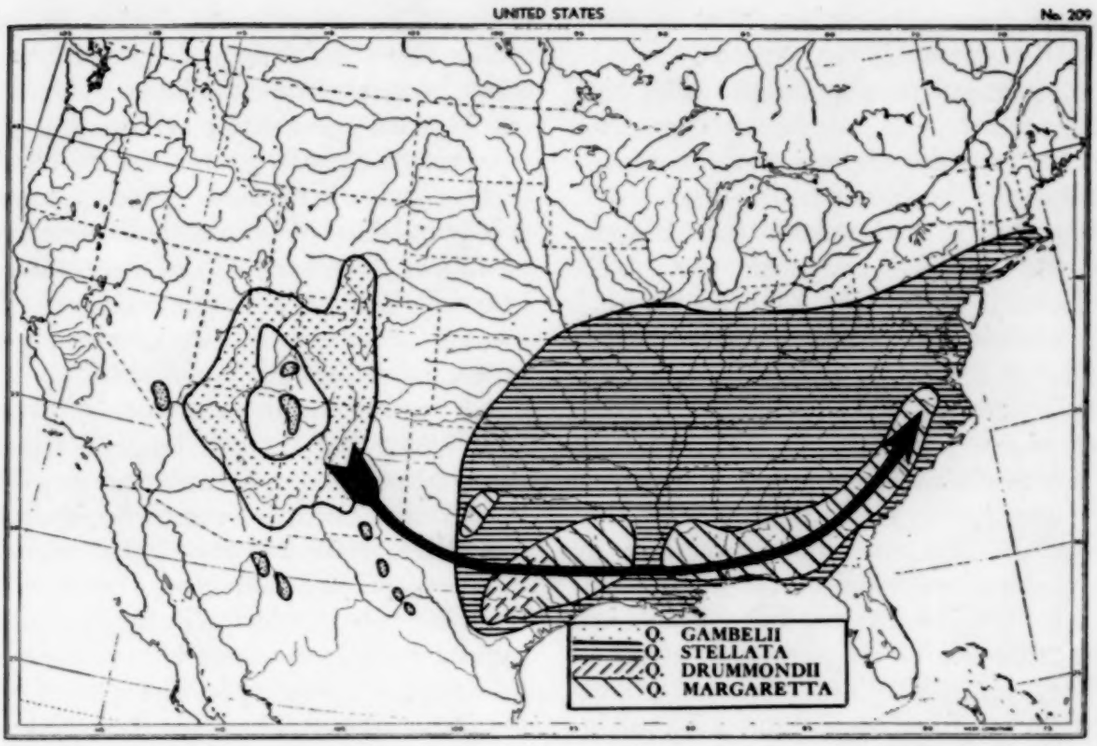

FIG. 3. Present (generalized) distributions of *Quercus Gambelii*, *Q. stellata*, *Q. Margaretta*, and *Q. Drummondii*. The arrow indicates the eastward migration of *Q. Gambelii* that gave rise to *Q. Margaretta* and *Q. Drummondii*.

so effective that the entire western end of the Coastal Plain populations have been rather uniformly enriched by *Q. stellata* genes. This population is what is known as *Q. Drummondii*. The lesser gene flow in the east has left the *Q. Gambelii* stock relatively unchanged so that the speciation of this population (as *Q. Margaretta*) has in large part resulted from its isolation from the ancestral *Q. Gambelii* and only slightly from hybridization with *Q. stellata*. The geographic relationships of these several species are shown in figure 3.

Although the small fruit and sometimes clavately lobed or even cruciform leaves of *Q. Margaretta* are suggestive of *Q. stellata*, the fundamental characters of *Q. Margaretta* reveal a close relationship to *Q. Gambelii*. The latter species shares with *Q. Margaretta* its glabrous brown twigs, red buds, persistent stipules, round-lobed leaves with usually narrow sinuses, glossy upper leaf surface, loosely spreading pubescence of the lower leaf surface, and short-peduncled fruit. Characters of *Q. stellata* appearing in *Q. Margaretta* populations may be ascribed to introgression since the earliest confluence of their ranges or they may indicate hybridization with *Q. stellata* superimposed upon accomplished speciation of *Q. Margaretta*. It is highly significant that the greatest incidence of *Q. stellata* characters occurs in the western end of the range of *Q. Margaretta* and progressively diminishes eastward.

The greater role of introgression in the origin of *Q. Drummondii* is revealed in several characters of that population. Tree habit, coarse twigs, heavy texture of leaf blades, and a tendency to shed the loose pubescence of the lower leaf surface which then becomes glaucous with the persistent bases of the deciduous hairs are all suggestive of *Q. stellata* influence. The remainder of the characters of *Q. Drummondii* are largely those common to *Q. Margaretta* and *Q. Gambelii*.

DISCUSSION

Mayr (1947, p. 268) poses some questions that may be at least partly answered

by these data. He writes, "Let us consider, for example, two spatially segregated, contiguous populations within a species which are not separated by an extrinsic barrier. Selection pressure will tend to pull these two populations apart, if they live in rather different habitats. But, can selection overcome the effects of dispersal across the zone of contact? Can conditioning reduce dispersal across the line of contact to such an extent that it no longer prevents the steady divergence of this population? Sufficient facts are not available for a decisive answer to these questions. The scanty evidence that is available indicates that speciation by geographical segregation (without isolation) is rare, if it occurs at all. Ecological differences are rarely abrupt in zones of primary intergradation. There is likely to be an intermediate habitat with an intermediate population to serve as a channel for the gene flow. In the cases where two ecologically very different subspecies are found in immediate contact, it can nearly always be shown that secondary contact is involved."

Mayr was thinking mostly of animal species, else he must immediately have seen in the more sedentary plant species a partial refutation of his argument. In genetically compatible sympatric plant species, such as *Quercus Havardi* and *Q. Mohriana,* swamping of one by the other is prevented by their great divergence in ecological requirements. The intermediate habitat and intermediate population indeed occur, but in this case they are strictly limited by the narrowness of the zone of mixture of sand and limestone. We are dealing here not with an actual case of evolution but with the maintenance of specific distinctness in spite of genetic compatibility and actual sexual contact. Distinctness is maintained as a consequence of ecological differences which are themselves sufficient basis for specific distinction.

If we consider the case of *Q. Margaretta,* the question is more clearly illuminated. *Quercus Gambelii* moved eastward to the Atlantic during the pluvial period that brought *Q. stellata* westward onto the Great Plains. The two species are genetically compatible but ecologically separated by the restriction of *Q. Gambelii* to sand. Thus the easterly population of *Q. Gambelii* underwent evolution (forming *Q. Margaretta*) by isolation with a minimum of gene flow from *Q. stellata.* Yet, in its westernmost range, this migrant *Q. Gambelii* shows a much stronger influence from *Q. stellata.* It is likely that a much longer period of contact may have increased the gene flow in this case, but it is extremely significant that there are in this area many extensive mixtures of clay and sand (intermediate habitats) upon which F_1 hybrids of *Q. stellata* and *Q. Margaretta* may currently be found in quantity. The evolution of *Q. Drummondii* from this extensive and aged hybrid swarm is thus the consequence of stability emerging as a result of *the great extent of the intermediate habitat.* In effect, ecological isolation was effected between the hybrid swarm and both of its parents.

Summary

Genetically compatible sympatric species are common in *Quercus.* The degree to which these hybridize successfully is dependent upon the factors that govern the survival of their hybrid offspring.

If the parent species differ radically in their soil requirements, the intermediate individuals survive only in an intermediate habitat formed by the mixing of the two soil types. For instance, *Q. Margaretta* is confined to deep sand and *Q. stellata* to adjacent areas of various clay and gravel or sandy clay substrata. Their hybrids occur on soils intermediate between these and do not penetrate the areas to which the respective parents are restricted.

Wide differences in climatic requirements also may minimize the effects of hybridization by restricting the degree of overlapping of ranges of parents. Thus *Q. Havardi,* an obligate inhabitant of deep

sand on the southern Great Plains, comes in actual contact with *Q. stellata* over a very limited area at the western extremity of the latter's range where they hybridize freely. Hybrids may be found as much as one hundred and fifty miles west of the present range of *Q. stellata*. The direction is contrary to the direction of the strong prevailing winds. It appears, therefore, that these outlying hybrids indicate the earlier extension of *Q. stellata* westward during a pluvial period of the Pleistocene.

These controls of effective hybridization played a part in the evolution of two species derived from *Q. Gambelii* (now confined to the Rocky Mountain region and southward and westward) and *Q. stellata* (now ranging from central Texas eastward and northward). *Quercus Gambelii* migrated eastward across the plains and along the sand areas of the Gulf Coastal Plain to the Atlantic during a pluvial period of the Pleistocene or earlier. Subsequent reduction of precipitation removed the plains population, thus isolating the Coastal Plain population from that of the mountains. The evolution resulting from this isolation has distinguished these populations, producing the Coastal Plain species known as *Q. Margaretta*.

Quercus Margaretta and *Q. stellata* are fully compatible, but their differences in soil requirements limit their gene exchange to a slow rate. However, the westernmost segment of the *Q. Margaretta* (née *Q. Gambelii*) population came in contact with *Q. stellata* in central Texas early in the eastward migration of *Q. Gambelii*. Furthermore, there exists in central Texas a larger area of intermediate habitats suitable to the hybrid progeny than is found east of the Mississippi River. As a consequence hybridization of *Q. Margaretta* with *Q. stellata* has been progressing in central Texas long and effectively. The resulting intermediate population has become fairly well stabilized and has formed what is known as *Q. Drummondii*.

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EVOLUTION OF THE CALIFORNIAN OAK *QUERCUS ALVORDIANA*[1]

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INTRODUCTION

Some years ago several herbarium specimens were noted that appeared to be intermediate, in varying degree, between the Blue Oak (*Quercus Douglasii* H. & A.) and Gray Oak (*Q. turbinella* Greene). These had been variously labelled—some of them as *Q. dumosa* var. *Alvordiana* (*Q. Alvordiana* Eastwood). The latter has long been a problematic entity among Californian oaks, and its taxonomic status has varied widely with different authors.

Quercus Douglasii and *Q. turbinella* characteristically occur in quite different ecological situations in California. The former is a deciduous tree restricted largely to foothills or lower mountain slopes bordering interior valleys. Its most common associate is the Digger Pine (*Pinus Sabiniana*) with which it forms an open woodland over extensive areas. Other less frequent woody associates are the Interior Live Oak (*Q. Wislizenii*) and Buck-brush (*Ceanothus cuneatus*). On the other hand, *Q. turbinella*, a small-leaved, evergreen shrub, occurs chiefly on dry slopes near or bordering the desert in southern California (its range extends eastward into Texas and southward into Mexico), or in the inner South Coast Ranges where the environment approaches desert-border conditions. It is commonly associated with the California Juniper (*Juniperus californica*) and in some areas with the One-leaf Piñon (*Pinus monophylla*) and Common Sagebrush (*Artemisia tridentata*). The ranges of *Q. Douglasii* and *Q. turbinella* overlap, however, in central and southern California, notably in parts of the inner South Coast Ranges (fig. 7).

The postulate was made that *Quercus Alvordiana*[2] has arisen through interbreeding between *Q. Douglasii* and *Q. turbinella*. More intensive work was undertaken in order to test this hypothesis, beginning with the study of numerous herbarium specimens of all three. This was followed by field study and the morphological analysis of a number of population samples ("mass collections"; cf. Anderson, 1941). These were collected in numerous areas where *Q. Alvordiana* occurs (its range being essentially coincident with the areas of overlap between *Q. Douglasii* and *Q. turbinella;* fig. 7), and also from areas where *Q. Douglasii*, on the one hand, and *Q. turbinella*, on the other, occur in a relatively "pure" state away from the region of overlap.

MORPHOLOGY

When a large number of herbarium specimens[3] was examined, two salient

[1] The present paper is a revision of part of a thesis submitted to the Graduate Division of the University of California in partial fulfillment of the requirements for the degree of Doctor of Philosophy. The writer wishes to express his thanks to Dr. Lincoln Constance, Dr. Herbert L. Mason, and Dr. G. Ledyard Stebbins, Jr., University of California, for their interest and encouragement during the progress of this study, and for their helpful advice and constructive criticism in the preparation of the manuscript.

[2] Throughout this paper this entity will be referred to as *Quercus Alvordiana*. Such usage is merely for convenience of reference, however, and it should be emphasized that the present author does not accord it the status of species. His views regarding its taxonomic disposition will be presented elsewhere (Tucker, in press).

[3] The writer is indebted to the curators of the herbaria at the following institutions, for the loan of specimens: University of Arizona; Arnold Arboretum, Harvard University; Cali-

facts became apparent. First, *Quercus Douglasii* and *Q. turbinella,* in areas away from their zone of overlap, exhibit a number of conspicuous morphological differences. Second, specimens from areas where their ranges overlap include a complete series of forms ranging from *Q. Douglasii* through *Q. Alvordiana* to *Q. turbinella.*

Table I summarizes the principal morphological (and ecological) differences between *Quercus Douglasii* and *Q. turbinella.*

A brief examination of leaf trichomes revealed differences which, at the outset, appeared quite distinct. To determine whether these were constant or not, a more comprehensive survey was undertaken, using the herbarium material that had been accumulated. This established the trichome differences noted in table I.

The lower (abaxial) surface of the leaf was found to be particularly favorable for this study. This surface in both species nearly always bears an indument in which stellate hairs occur. In *Quercus Douglasii* this type predominates, but in *Q. turbinella,* smaller, uniseriate, one- to several-celled glandular hairs may be equally abundant. Glandular hairs may be found in *Q. Douglasii* also, but at best they form only a small part of the indument. In both oaks the stellate hairs are quite variable, although those of *Q. Douglasii* tend to be longer and sparser than those of *Q. turbinella,* and usually have

fornia Academy of Sciences; University of California, Berkeley; University of California, Los Angeles; Pomona College; San Diego Museum of Natural History; Stanford University; U. S. National Museum; Utah State Agricultural College; and the Vegetative Type Map Herbarium, Berkeley.

TABLE I

	Quercus Douglasii	*Quercus turbinella*
Natural habitat	Foothills of interior valleys	Semi-arid slopes bordering desert areas
Habit	Tree, moderate to rather small (7 m. tall)	Shrub, rarely a small shrubby tree (to 5 m. tall)
Twigs of current year's growth		
Pubescence	Glabrate to usually moderately pubescent (occasionally densely so)	Densely short-tomentose
Color	Brown to light brownish	Yellowish
Mature terminal buds		
Size	2.0–6.6 (or more) mm. long × 1.9–3.2 (or more) mm. wide	1.0–2.2 mm. long × .7–1.8 mm. wide
Shape	Ovoid to broad-ovoid	Globose to sub-globose
Mature leaves		
Size	30–70 (rarely 90) mm. long × 15–40 mm. wide	15–35 (rarely 40) mm. long × 10–25 mm. wide
Margin	Crenate-dentate or -lobed to entire	Spinose-dentate
Trichomes of lower surface	Stellate hairs with few rays (5 or fewer, commonly 4), commonly erect or spreading, often rather sparse	Stellate hairs with 7 or more rays (commonly 8), commonly appressed and densely crowded
	Uniseriate glandular hairs scanty or absent; when present, not yellow	Uniseriate, yellow glandular hairs common, often abundant
Color of upper surface	Bluish-green	Gray to grayish-green
Persistence	"Deciduous"	"Evergreen"

ascending rays. The stellate hairs of the latter are often crowded, with appressed or laterally spreading rays. Before the survey was begun, the specimens were segregated on the basis of gross morphological characters and location data, into the following seven convenient categories:

A. "Good" *Quercus Douglasii* from areas outside the range of *Q. Alvordiana* (32 specimens);

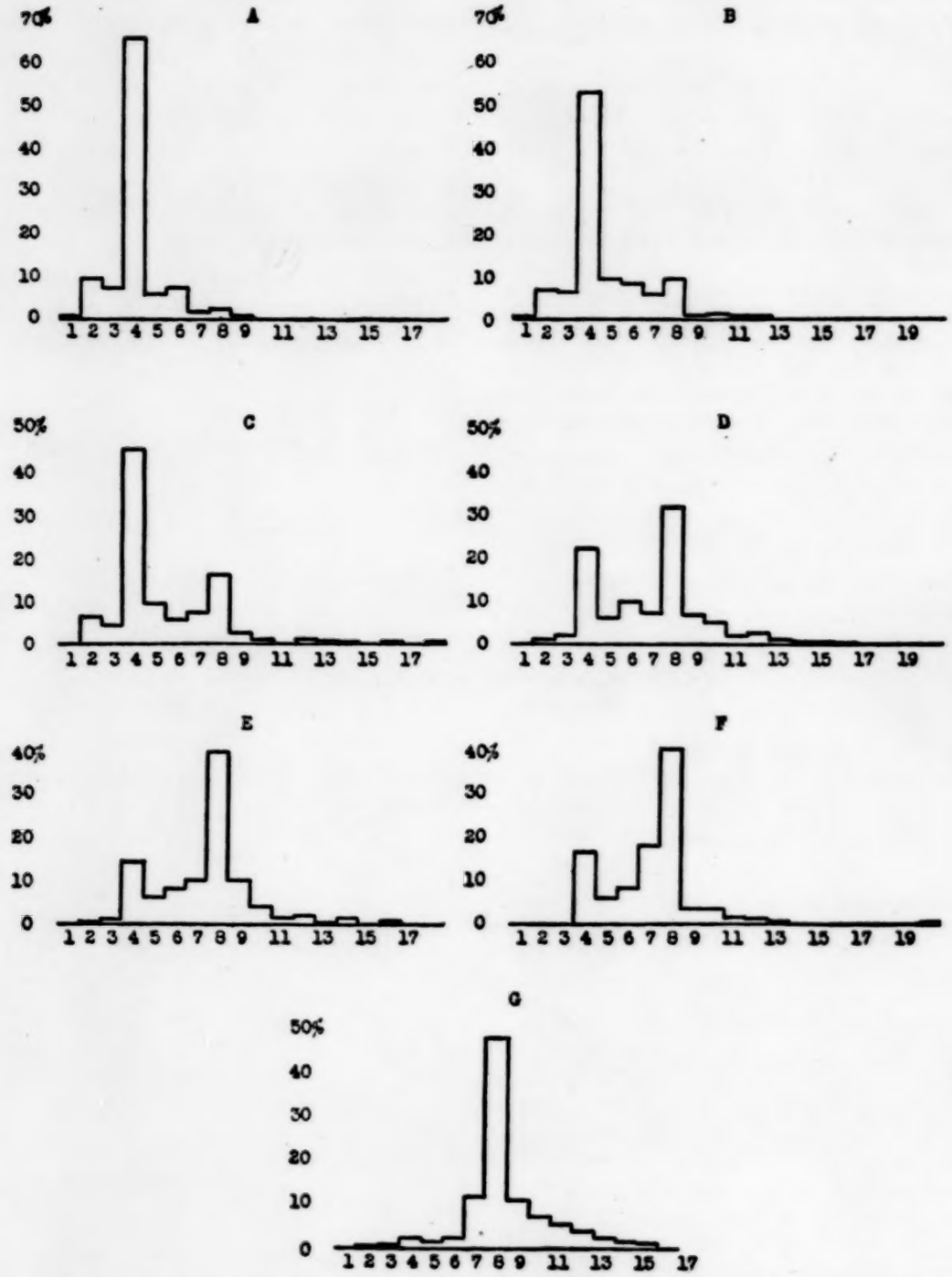


FIG. 1. Ray numbers in stellate trichomes of *Quercus Douglasii*, *Q. Alvordiana*, and *Q. turbinella*. (In each case, horizontal scale indicates number of rays per trichome; vertical scale indicates percentage of all trichomes examined for that category; categories A–G explained in text.)

B. "Good" *Q. Douglasii* from areas adjacent to, or within the range of *Q. Alvordiana* (69 specimens);
C. "Aberrant" *Q. Douglasii* from areas within the range of *Q. Alvordiana* (46 specimens);
D. *Q. Alvordiana,* i.e., specimens more or less intermediate in general morphological characters (30 specimens);
E. "Aberrant" *Q. turbinella* from areas within the range of *Q. Alvordiana* (38 specimens);
F. "Good" *Q. turbinella* from areas adjacent to, or within the range of *Q. Alvordiana* (48 specimens);
G. "Good" *Q. turbinella* from areas outside the range of *Q. Alvordiana* (87 specimens).

For this analysis, a single characteristic leaf was taken from each specimen in turn. Using reflected light, the under side near the base (approximately the basal ¼ of the leaf) was examined with a compound microscope. Ten trichomes, chosen at random, were carefully scrutinized and the ray number recorded for each. Whenever possible, all ten were chosen from a single low power (100 ×) field. The aggregate data for all the specimens in each of the seven categories are presented as a single histogram (fig. 1, A–G).

The results of this survey may be summarized as follows.

1. The predominant ray number for stellate hairs of the lower leaf surface of *Quercus Douglasii* is 4 (histogram A).

2. The predominant ray number in *Q. turbinella* is 8, although higher numbers are common (histogram G).

3. The ray number in *Q. Alvordiana* is more or less intermediate (histogram D).

4. Except for the two extreme categories, A and G (and possibly B), the histograms show two significant modes, these being at 4 and 8. Progressing from A to C, the mode at 4 decreases and the mode at 8 increases. This modification of *Q. Douglasii* in the direction of *Q. turbinella* could be explained by assuming the infiltration of *Q. turbinella* genes into *Q. Douglasii* in areas where they overlap, through hybridization and backcrossing (introgression). Conversely, *Q. turbinella* from such areas has been modified in the direction of *Q. Douglasii,* for in histograms E and F the mode at 4 is larger than, and the mode at 8 smaller than in histogram G. Again, this could be the result of introgression.

A less extensive survey was made of the glandular trichomes. Considerable variability was noted, but it was found that in *Quercus turbinella,* especially from outside the range of *Q. Alvordiana,* they are usually golden-yellow and quite abundant. In *Q. Douglasii* they are generally much less abundant and have either a colorless, silvery appearance, or in age, a dark brown color. *Quercus Alvordiana* was found to be intermediate, at least with respect to relative abundance.

Relative Length of Leaf Persistence

As noted previously, *Quercus Douglasii* is typically deciduous, while *Q. turbinella* is evergreen. Field observations of leaf persistence were made during a short period from December 28, 1947, to January 3, 1948. A total of seventeen different populations was observed, including *Quercus Douglasii, Q. turbinella,* and *Q. Alvordiana.* At each location twenty-five individuals (in three cases, smaller numbers) were selected at random. First, each was classified as to its degree of deciduousness: (1) completely deciduous or nearly so, (2) retaining a small amount of foliage, (3) retaining a considerable amount of foliage, or (4) retaining much or all of the foliage. Secondly, on the basis of general morphological characteristics, each was classified as *Q. Douglasii, Q. Alvordiana,* or *Q. turbinella.* In cases of complete deciduousness, leaf characters of an individual were determined from leaves on the ground directly beneath it. The data obtained are given in table II.

TABLE II

Location number	No. individuals observed	Taxonomic classification			Degree of deciduousness			
		% classified as *Q. Douglasii*	% classified as *Q. Alvordiana*	% classified as *Q. turbinella*	% completely deciduous (or nearly so)	% retaining a small amount of foliage	% retaining a considerable amount of foliage	% retaining much or all of foliage
8*	25	100	0	0	96	4	0	0
9*	25	100	0	0	60	36	4	0
16*	25	100	0	0	68	24	8	0
17*	25	100	0	0	96	4	0	0
13**	17	100	0	0	53	41	6	0
14	25	92	8	0	36	44	20	0
1	25	92	8	0	36	28	32	4
15	25	68	32	0	28	36	32	4
5	25	36	64	0	44	52	0	4
2	21	29	71	0	28	67	5	0
10	25	20	80	0	16	28	36	20
6	24	20	80	0	42	21	29	8
3	25	0	100	0	8	60	28	4
11	25	8	24	68	4	4	72	20
7	25	0	20	80	0	32	64	4
4**	25	0	0	100	0	12	76	12
12**	25	0	0	100	0	0	4	96

* Populations in areas well outside the range of *Quercus Alvordiana*.
** Populations in areas outside, but adjacent to the range of *Quercus Alvordiana*.

Several factors tend to limit the value of these data: (1) the effects of fall and winter winds may have varied from population to population; (2) the four categories of deciduousness recognized were not susceptible of sharp delimitation; and (3) the degree of deciduousness was judged by the crude process of making rough, visual estimates. Nevertheless, it is evident that the populations which are largely or completely *Quercus Alvordiana*, although rather variable, are, in general, intermediate in this character.

POPULATION SAMPLES

Following preliminary field study, a series of population samples was collected, not only throughout the range of *Quercus Alvordiana*, but also in areas where *Q. Douglasii*, on the one hand, and *Q. turbinella*, on the other, occur in a relatively "pure" state. Thirty-five collections of about 25 individuals each were made in the fall of 1948. In order to have material that would be comparable for fruit and bud characters, these were made over as brief a time span as possible in late September and early October. Used in this study also was one collected in October, 1946, and three smaller population samples collected in the fall of 1947. The total thus came to thirty-nine collections (table III).

These population samples were analyzed following the hybrid index method used by Anderson (1936) and others (Goodwin, 1937; Heiser, 1947; Stebbins, Matzke, and Epling, 1947). An index was developed based on six of the most constant differences between *Quercus Douglasii* and *Q. turbinella*—those of growth habit, bud shape, leaf size, leaf margin, stellate trichomes, and leaf color (see table I). Each character of *Q. Douglasii* was assigned an index score of 0; each character of *Q. turbinella*, a score of 2; and the intermediate condition, a score of 1.

While scoring the qualitative characters other than habit, "standard" specimens for the condition of each character were kept at hand for judging the material. It should be pointed out that the "standard" specimens of *Quercus turbinella* were

TABLE III. *Population samples of* Quercus Douglasii, Q. Alvordiana, *and* Q. turbinella

Collection number (all coll. by author)	No. of individuals in sample	Location
A. *Quercus Douglasii* from areas outside the range of *Q. Alvordiana*		
1869	26	11.3 mi. w. of Williams, Colusa Co.
1870	25	1.3 mi. w. of Guinda, Yolo Co.
1868	28	So. side Hiway 12, ca. ¼ mi. e. of Sonoma-Napa Co. line, in Napa Co.
1787	25	Ca. 6 mi. se. of Copperopolis, Calaveras Co.
1786	26	1 mi. sw. of Jamestown, Tuolumne Co.
1893–1894	27	3 mi. se. of Livermore, Alameda Co.
1897	25	Del Puerto Canyon, 19 mi. (by road) w. of Patterson, Stanislaus Co.
1898	26	E. side of Pacheco Pass, Merced Co.
B. *Q. Douglasii* from areas adjacent to, or within the range of *Q. Alvordiana*		
1899	26	5.2 mi. w. of Llanada, San Benito Co.
1890	25	Beside road from Parkfield to Coalinga, 4.2 mi. so. of Parkfield Jct., Fresno Co.
1915	25	.4 mi. so. of road from Bradley to Lockwood, ca. 12 mi. w. of Bradley, Monterey Co.
1888	26	3.9 mi. n. of Cholame, San Luis Obispo Co.
1632–1640	16	Ca. ¼ mi. so. of Hiway 466, ca. 6 mi. e. of Cholame, San Luis Obispo Co.
1627	13	So. side Hiway 166, in San Luis Obispo Co., 16.7 mi. (by road) e. of Pine Canyon Guard Station.
1884	27	San Emigdio Canyon, 5.1 mi. above San Emigdio Ranch headquarters, Kern Co.
1871	25	Near Hiway 466, 7.5 mi. (by road) nw. of Tehachapi, Kern Co.
C. Intermediate or mixed populations (*Q. Alvordiana*, at least in part)		
1919	25	13.3 mi. (by road) w. of Greenfield, beside road to Jamesburg, Monterey Co.
1918	25	13.3 mi. (by road) w. of Greenfield, beside road to Jamesburg, Monterey Co.
1913	26	W. side of Hiway 101, 5 mi. so. of San Ardo, Monterey Co.
1914	24	8.8 mi. w. of Bradley, Monterey Co.
1900	26	7 mi. so. of Panoche, San Benito Co.
1901	25	7.3 mi. so. of Panoche, San Benito Co.
1911	26	Ca. 8 mi. se. of Idria, San Benito Co.
1892	26	Beside road from Parkfield to Coalinga, .8 mi. so. of Parkfield Jct., Fresno Co.
1891	27	Beside road from Parkfield to Coalinga, 2.6 mi. so. of Parkfield Jct., Fresno Co.
1887	26	15 mi. (by road) w. of McKittrick, Kern Co.
1883	26	San Emigdio Canyon, 6.5 mi. above San Emigdio Ranch headquarters, Kern Co.
1881	25	San Emigdio Canyon, 7 mi. above San Emigdio Ranch headquarters, Kern Co.
1880	26	Ca. 9.6 mi. e. of Gorman, Los Angeles Co.
1873	26	Oak Creek, 13.8 mi. w. of Mojave, Kern Co.
1872	24	Ca. 9 mi. e-se. of Tehachapi, Kern Co.
D. *Q. turbinella* from areas adjacent to, or within the range of *Q. Alvordiana*		
1912	25	Beside San Benito River, 26.9 mi. (by road) nw. of Coalinga, in San Benito Co.
1917	25	11.4 mi. s. of King City, Monterey Co.
1886	24	Ca. 2 mi. ne. of summit of Caliente Mtn., San Luis Obispo Co.
1885	26	Salisbury Canyon, 9.1 mi. so. of Hiway 166, Santa Barbara Co.
1467	30	Near Hiway 99, ca. 3 mi. so. of Lebec, in Los Angeles Co.
E. *Q. turbinella* from areas outside the range of *Q. Alvordiana*		
1876	26	New York Mountains, ca. 8 mi. so. of Ivanpah, San Bernardino Co.
1875	26	New York Mountains, ca. 8 mi. so. of Ivanpah, San Bernardino Co. (ca. ½ mile from No. 1876)

selected from the two population samples from the New York Mountains, Nos. 1875 and 1876. Since the author now considers this material to be subspecifically distinct from the species population of the inner South Coast Ranges, etc., it might have been preferable to select "standards" from the "purest" material at hand from the latter area. However, the differences between the two subspecies involve characters other than those used in the index separating *Q. turbinella* and *Q. Douglasii*. Hence, it seems likely that the "standards" would have been very nearly the same for these index characters regardless of the subspecies from which they were chosen.

Leaves of *Quercus Douglasii* from areas outside the range of *Q. Alvordiana* are, on the average, distinctly larger than those of *Q. turbinella* from areas where the latter is "pure." Scatter diagrams for leaf size prepared from miscellaneous herbarium specimens of *Q. Douglasii* and *Q. turbinella*, however, showed some overlap between the smaller values for the former and the larger values for the latter. A comparison between the scatter diagrams for population samples of *Q. Douglasii* and *Q. turbinella* showed a smaller overlap, even when the sample of "pure" *Q. Douglasii* with the lowest minimum (No. 1897), and the sample of "pure" *Q. turbinella* with the highest maximum (No. 1875) were compared. This difference was not surprising, for, as Lewis (1947) has emphasized, a series of individual herbarium specimens, collected over a period of many years, might be expected to show the range of variation for a species as a whole better than even a considerable number of "mass collections" made in a single season. For the purpose of distinguishing three categories—*Quercus turbinella*, intermediate, and *Q. Douglasii*—only data from the two "mass collections" mentioned above (Nos. 1897 and 1875) were considered. Their zone of overlap was designated as the intermediate range for the scoring index. On this basis, only two individ-

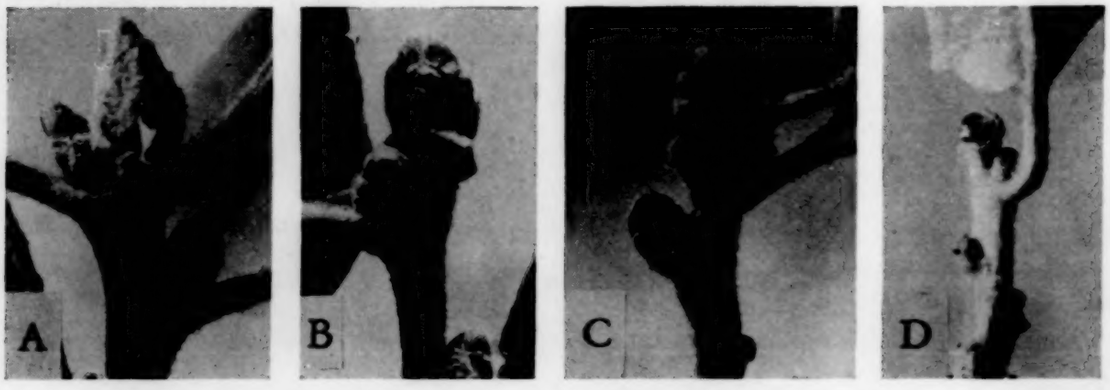


FIG. 2. Bud shapes characteristic of *Quercus Douglasii*, *Q. turbinella*, and the intermediate condition. A and B. Extremes of the range of variation scored as *Q. Douglasii* (A. Tucker No. 1787–22, B. Tucker No. 1786–4), C. The intermediate condition (Tucker No. 1786–10), D. *Q. turbinella* (Tucker No. 1875–20). All × ca. 4.

Habit data were obtained for most of these population samples, but only incompletely or not at all for the remainder, in which case the collection was scored only on the other five characters. Thus total index values range from 0 to 12 in population samples for which habit data were obtained, and from 0 to 10 in the others.

Bud shape and leaf color, particularly, were difficult to evaluate in some collections. This was due not only to frequent "border-line" cases, but also to the variability of individual specimens. Bud shapes characteristic of *Quercus Douglasii*, *Q. turbinella*, and the intermediate condition, are shown in figure 2.

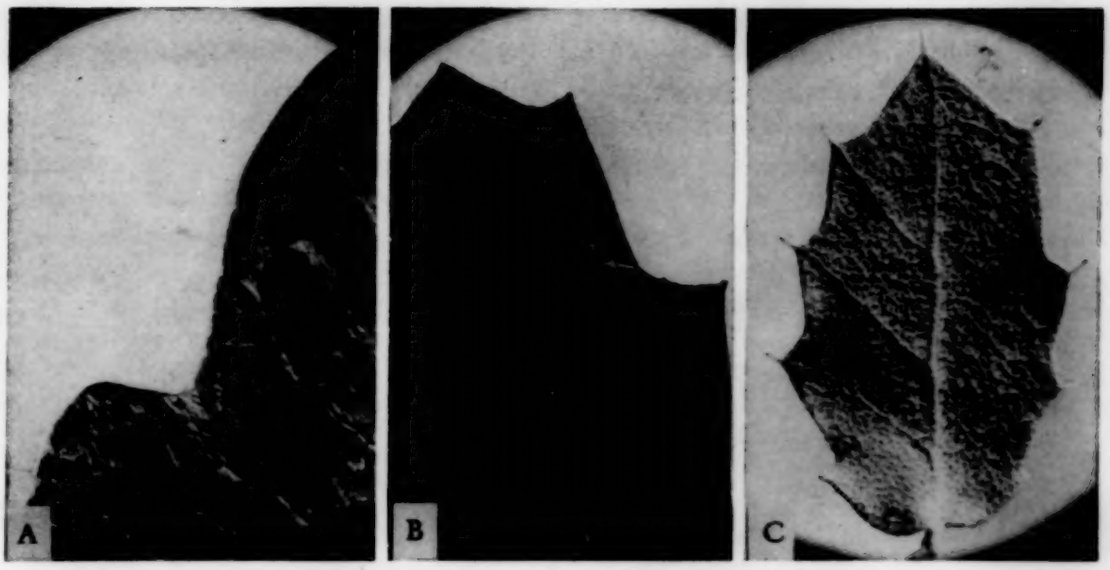


FIG. 3. Leaf margins characteristic of A. *Quercus Douglasii* (Tucker No. 1869–10), B. The intermediate condition (Tucker No. 1618), and C. *Q. turbinella* (Tucker No. 1876–9). All × ca. 3.

uals in the *Q. Douglasii* sample (8%) fell within this intermediate range. In the *Q. turbinella* sample four individuals (15%) fell within this range.

The types of leaf margin and stellate trichome characteristic of *Quercus Douglasii, Q. turbinella,* and the intermediate condition, are shown in figures 3 and 4, respectively. In trichome analyses of these collections, a larger sample (30–50 trichomes) from each specimen was examined than in the previously discussed study, in order to obtain more significant data. Here again, the results showed some variability. For scoring purposes, after testing various possibilities, the following procedure was adopted: (1) if 70% or more of the trichomes examined

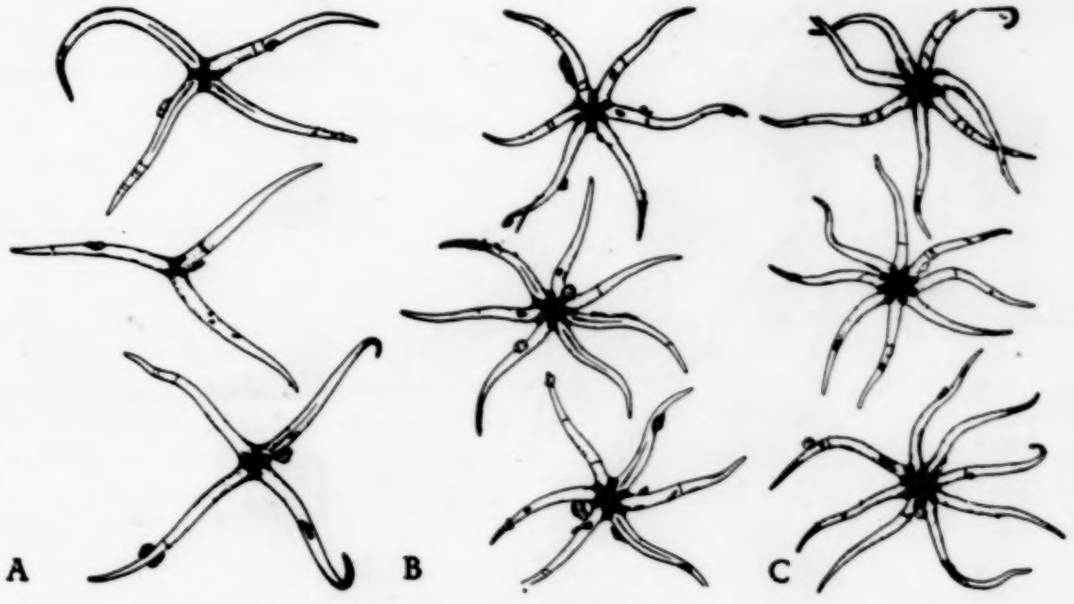


FIG. 4. Drawings of stellate trichomes characteristic of A. *Quercus Douglasii* (R. Tofsrud, July 12, 1948), B. The intermediate condition (the type of *Q. Alvordiana,* California Academy of Sciences 1034), and C. *Q. turbinella* (C. H. Muller No. 8227). All × ca. 110.

on one individual had five or fewer rays, it was scored as *Q. Douglasii;* (2) if 70% or more had seven or more rays, it was scored as *Q. turbinella;* and (3) any other condition was scored as intermediate.

Data for another difference listed in table I—size of mature terminal buds—were compiled for all population samples. It was noted that the scatter patterns of bud size and leaf size for a given population sample were usually quite similar. It seemed possible that this marked correlation might be due to some single underlying phenomenon—perhaps a complex of growth processes influencing cell development in foliar appendages throughout the plant. Anderson and Ownbey

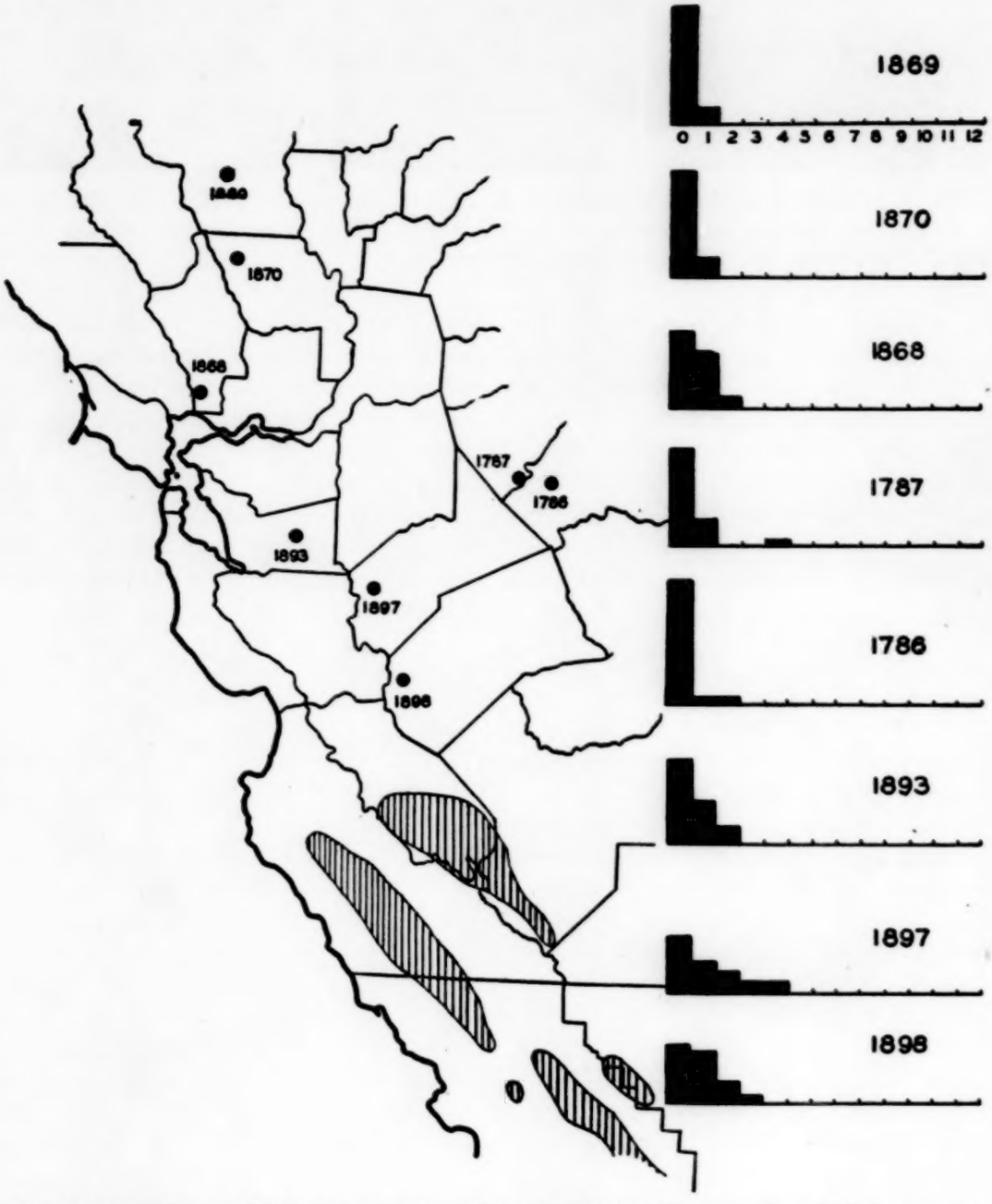


FIG. 5. Locations and histograms for population samples of *Quercus Douglasii* from areas outside the range of *Q. Alvordiana.* (See text for explanation of histograms). Distribution of *Q. turbinella* is indicated by shaded areas.

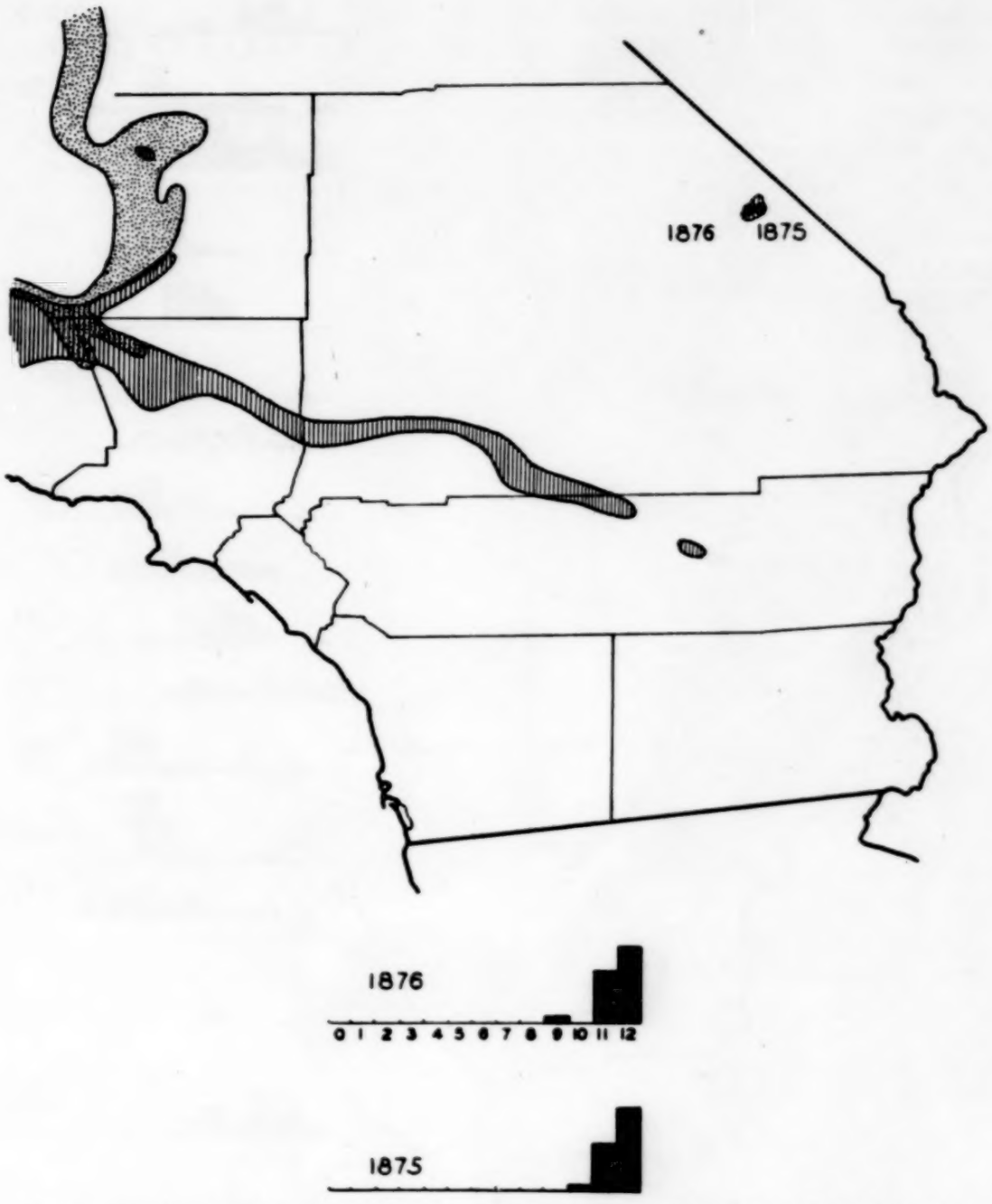


FIG. 6. Locations and histograms for population samples of *Quercus turbinella* from areas outside the range of *Q. Alvordiana.* (See text for explanation of histograms.) Distribution of *Q. Douglasii* is indicated by stippled area, *Q. turbinella* by shaded area.

(1939) found evidence of such phenomena in studies made on two different species of *Nicotiana.* Of course, a winter bud is not a single structure as is a leaf. Still, it is conceivable that such growth processes, exerting similar effects on both foliage leaves and cataphylls, might have a similar effect, indirectly, on the entire bud. Hence, it was deemed better not to regard bud size and leaf size as independent characters, nor to use them both in the hybrid index, for this would give undue weight to the size of foliar structures. Consequently only leaf size was used.

As a basis for interpreting populations of *Quercus Alvordiana,* the results obtained for collections of the putative par-

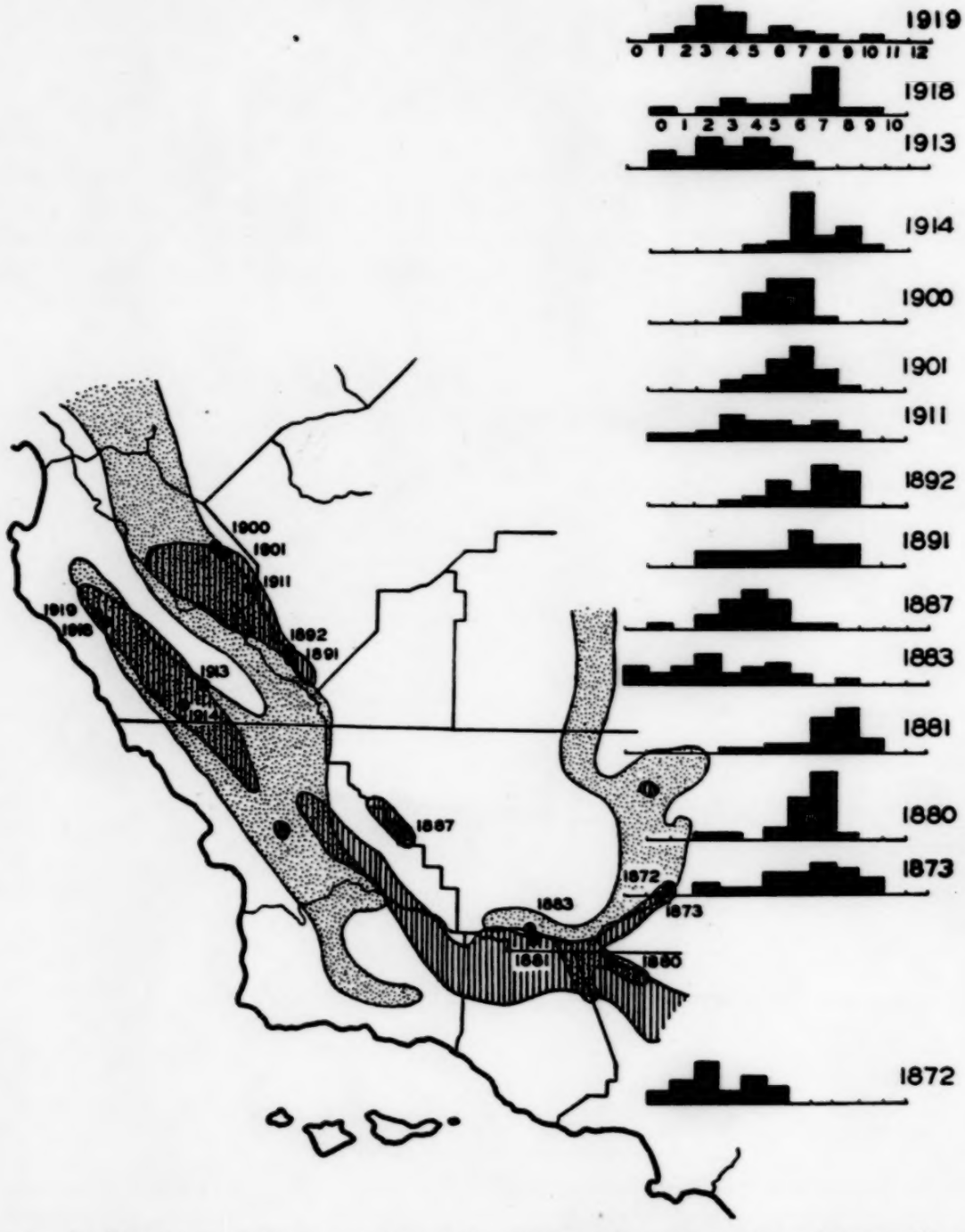


FIG. 7. Locations and histograms for samples of intermediate or mixed populations. (See text for explanation of histograms.) Distribution of *Quercus Douglasii* is indicated by stippled areas, *Q. turbinella* by shaded areas.

ents from areas outside their zone of overlap will be studied first. For the sake of discussion and comparison, the four lowest classes of totals, 0–3 inclusive, are designated as "good" *Q. Douglasii,* for an overwhelming majority of the individuals in collections of the latter fall in this range (fig. 5; index totals shown by horizontal scale, number of plants shown by heights of vertical columns). An equal range, comprising the classes 9–12 inclusive, is designated as "good" *Q. turbinella,* for all the totals of both collections from the New York Moun-

tains fall in this range (fig. 6). The classes 4–8 inclusive, are, of course, "intermediate." These ranges apply in collections whose index totals run from 0 to 12. In collections in which they run from 0 to 10, the range, 0–2 inclusive, will indicate "good" *Q. Douglasii,* and 8–10 inclusive, "good" *Q. turbinella.*

In figure 7 striking diversity is apparent. This is shown by the group of population samples as a whole, for in some (e.g., No. 1919), the bulk of the

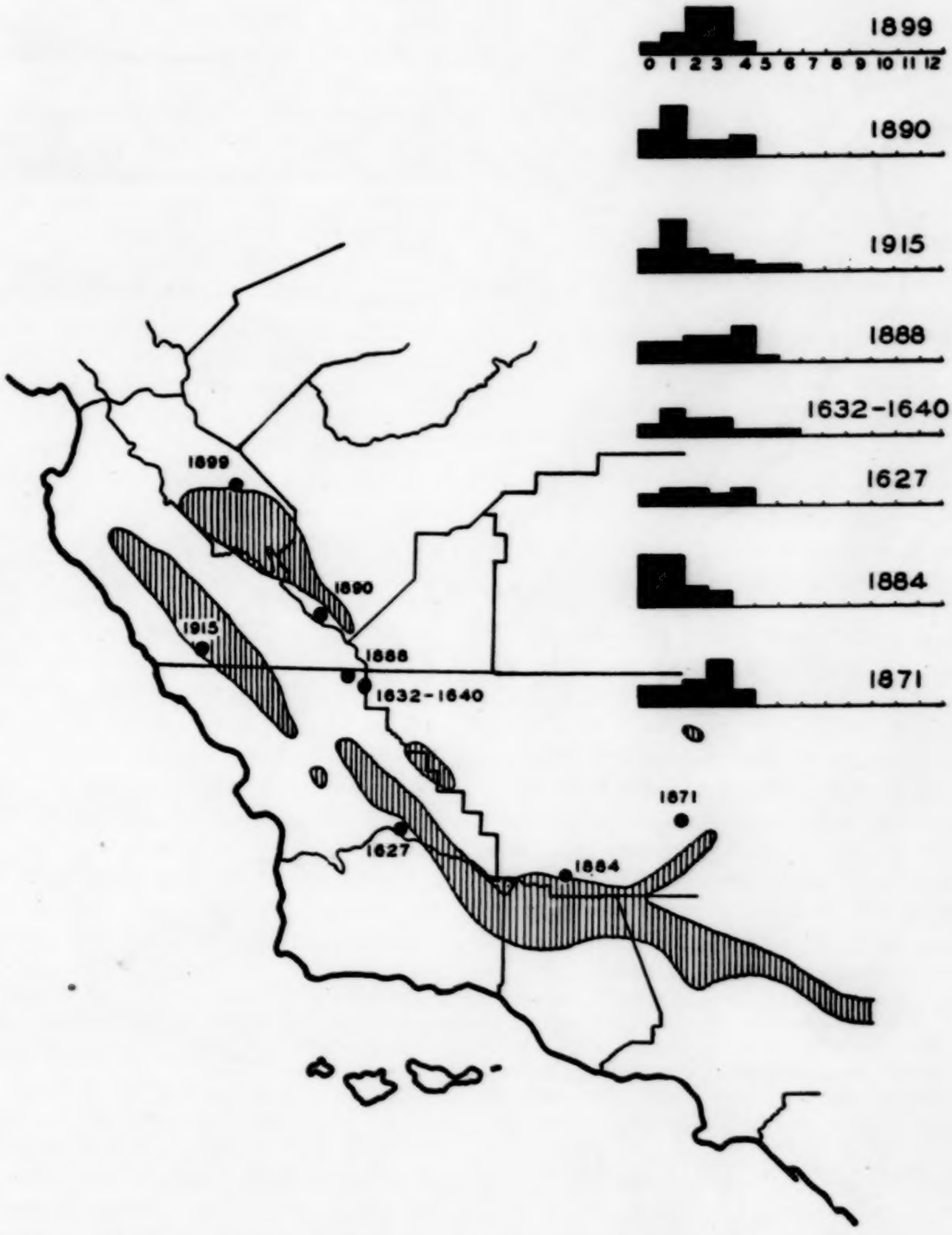


FIG. 8. Locations and histograms for population samples of *Quercus Douglasii* from areas adjacent to, or within the range of *Q. Alvordiana.* (See text for explanation of histograms.) Distribution of *Q. turbinella* is indicated by shaded areas.

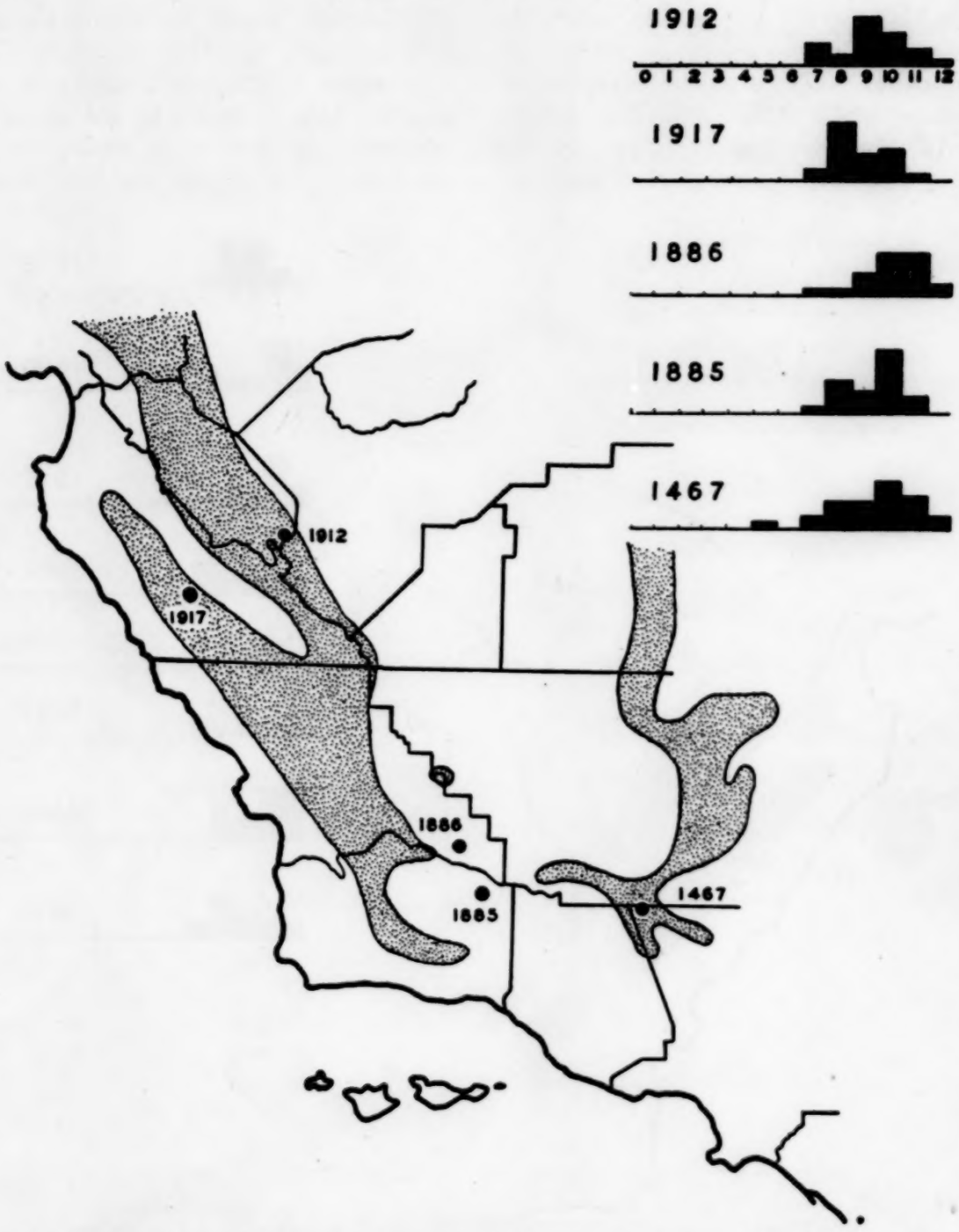


FIG. 9. Locations and histograms for population samples of *Quercus turbinella* from areas adjacent to, or within the range of *Q. Alvordiana*. (See text for explanation of histograms.) Distribution of *Quercus Douglasii* is indicated by stippled areas.

index totals lies on the *Q. Douglasii* side; in others (e.g., No. 1881), on the *Q. turbinella* side; and in a few (e.g., No. 1900), at or near the middle of the intermediate range. Moreover, within a number of the individual samples, a high degree of diversity is indicated by the broad range of index classes spanned. As the map indicates, these intergrading or intermediate populations have been noted in the inner South Coast Ranges as far north as central San Benito County, on the west

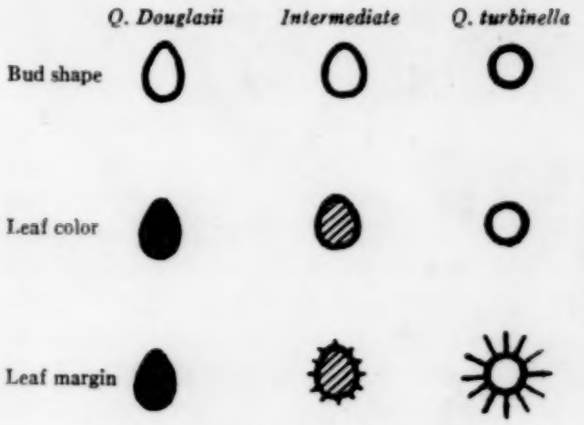
side of the Salinas watershed in Monterey County, in the Tehachapi Range, and elsewhere.

In populations of Category B (fig. 8), greater diversity than in Category A (fig. 5) is indicated by the broader range of classes. This, coupled with the fact that the modes of all the histograms in figure 8 lie nearer the intermediate range, indicates that *Quercus Douglasii* within, or near the range of *Q. Alvordiana,* is, in general, modified in the direction of *Q. turbinella.* To casual observation in the field, however, such populations, save for smaller leaf size, seemed scarcely different from the typical blue oak of farther north, outside the range of *Q. Alvordiana.*

In Category D (fig. 9), finally, it is evident that these populations of *Quercus turbinella* are somewhat modified (as compared with those of fig. 6) in the direction of *Q. Douglasii.*

As in the case of *Quercus Douglasii,* populations of *Q. turbinella* in or near the zone of overlap, usually seemed little different in the field, from those away from it. Leaf color, however, was often darker green in the more northerly collections of Category D (Nos. 1912 and, especially, 1917) than in the southernmost (No. 1467). In some populations of *Q. turbinella* in the hills west of the Salinas Valley in Monterey County, the upper leaf surface was often distinctly glossy, in addition to being darker green. Both these characters typify *Quercus dumosa* Nutt., an oak closely related to *Q. turbinella.* In populations where the two characters appear together, it may be that genes of *Q. dumosa* (which probably occurs in the general area) are involved. This interesting situation deserves a more detailed study.

Histograms furnish information about *populations,* but provide very little about the *individuals* making up the populations. In order to determine the patterns of correlation between five index characters within these various populations, a series of pictorialized scatter diagrams (Anderson, 1949) was prepared.



Classification of Stellate Trichomes

I. 86–100% of trichomes examined having 5 or fewer rays.
II. 70–85% of trichomes examined having 5 or fewer rays.
III. Less than 70% of trichomes examined having 5 or fewer rays, but more trichomes in this range than in the range, 7 or more.
IV. Less than 70% of trichomes examined having 7 or more rays, but more trichomes in this range than in the range, 5 or fewer.
V. 70–85% of trichomes examined having 7 or more rays.
VI. 86–100% of trichomes examined having 7 or more rays.

FIG. 10. Explanation of symbols used in pictorialized scatter diagrams.

Anderson has stated that "When well-differentiated entities hybridize, we may expect their cohesive forces to continue to operate for many successive generations in hybrid swarms. Certainly for scores, and perhaps for hundreds, of generations, we may expect to find the characters that went into the cross together still *tending* to stay together" (*op. cit.,* p. 93). This view is based on the tenets that species crosses involve large numbers of gene differences, and that linkage exerts a powerful cohesive force tending to retain parental gene combinations and greatly restrict the number of recombination types that might be produced.

The author's pictorialized scatter diagrams (for explanation of symbols used, see fig. 10) show patterns of recombinations that seem to support Anderson's thesis only weakly, at best. In populations containing both parental types and various intermediates (e.g., No. 1918,

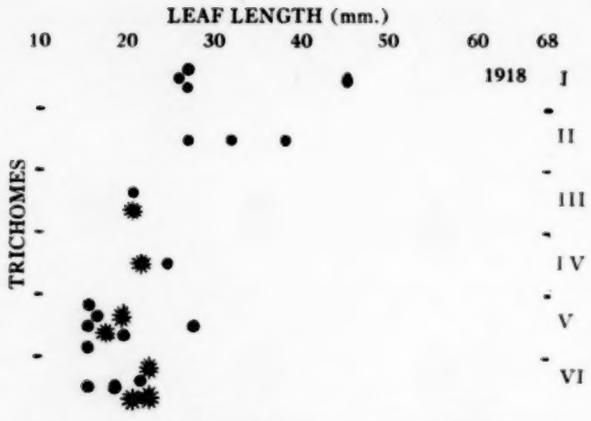


FIG. 11. Pictorialized scatter diagram for population sample No. 1918. See table III for location.

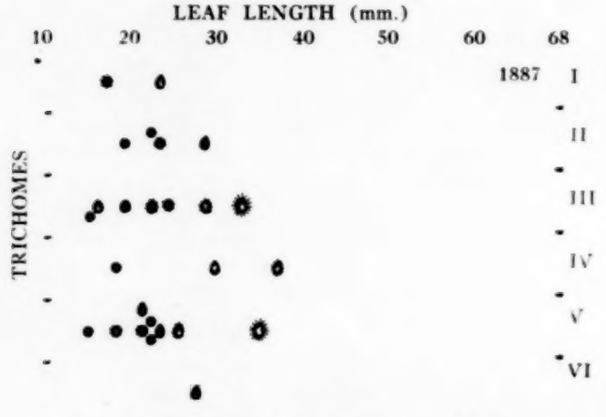


FIG. 12. Pictorialized scatter diagram for population sample No. 1887. See table III for location.

fig. 11), the scatter diagrams conform only in a rather indistinct fashion to the "recombination spindle" postulated by Anderson. Furthermore, in populations more intermediate in character (e.g., No. 1887, fig. 12), there seems to be no suggestion of a "recombination spindle," and the parental characters are thoroughly "shuffled" and recombined. (For scatter diagrams of both parents, see figs. 13 and 14. For scatter diagrams of other populations, see Tucker, 1950.) Since some rather extreme recombination types occur in these populations, it may be that the character differences between the parents may be determined by a relatively smaller number of genes than Anderson has assumed to be generally the case. The number of generations of interbreeding in these cases is, of course, unknown, and in some, may be very large. Still, the evidence from progeny tests of oak hybrids likewise suggests (Stebbins, 1950, pp. 64–65) that the number of genes by which oak species differ is smaller than in most other genera. In this case, therefore, and possibly in other cases of hybridization in *Quercus,* interspecific differences may be obliterated in a smaller number of generations than in other Angiosperm genera.

PALEOBOTANICAL AND GEOLOGICAL EVIDENCE

Information relating to the history of *Quercus Alvordiana* is very incomplete. In fact, no fossil oak referable to *Q. Alvordiana* itself has yet been found (D. I. Axelrod, written communication, 1948). Several occurrences of the presumed pre-

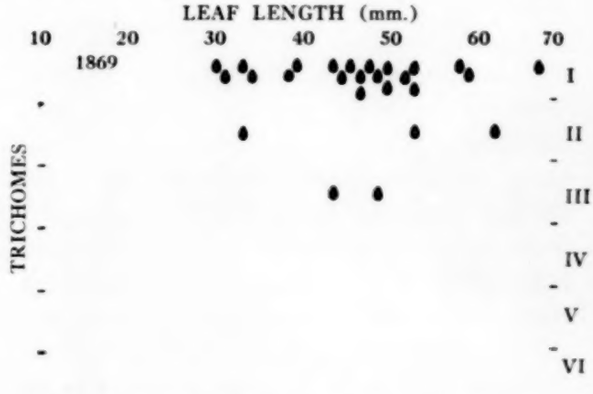


FIG. 13. Pictorialized scatter diagram for population sample No. 1869. See table III for location.

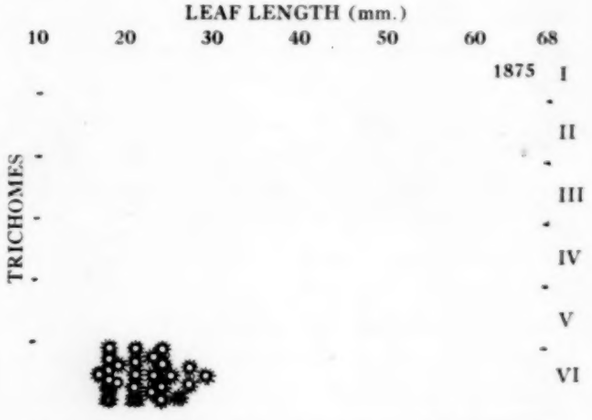


FIG. 14. Pictorialized scatter diagram for population sample No. 1875. See table III for location.

decessors of both *Q. turbinella* and *Q. Douglasii,* however, have been recorded from later Tertiary deposits in California. Their sympatric existence, moreover, appears to have been a distinct possibility at least since Lower Pliocene time. (Their occurrence together in the Middle Pliocene Oakdale flora is, as indicated below, a matter of record.)

The records of *Quercus dispersa* (Lesquereux) Axelrod, the Tertiary equivalent of *Q. turbinella,*[4] are as follows:

1. Tehachapi flora, Kern County: Middle Miocene (Axelrod, 1939).
2. Mint Canyon flora, Los Angeles County: uppermost Miocene (Axelrod, 1940).
3. Upper Puente flora, Los Angeles County: Upper Miocene (Axelrod, 1940) or transitional Mio-Pliocene (Chaney, 1944; table 33).
4. Table Mountain flora, Tuolumne County: transitional Mio-Pliocene (Condit, 1944b). In the opinion of the present author, the single leaf cited (which he has examined) appears to be a small leaf of *Q. convexa* Lesquereux, the Tertiary equivalent of *Q. Engelmannii* Greene, which was well-represented in this flora.
5. Oakdale flora, Stanislaus County: Middle Pliocene (Axelrod, 1944a).

The records of *Quercus douglasoides* Axelrod, the Tertiary equivalent of *Q. Douglasii,* are as follows:

1. Remington Hill flora, Nevada County: transitional Mio-Pliocene (Condit, 1944a).
2. Oakdale flora (listed above).
3. Mount Eden flora, Riverside County: Middle Pliocene (Axelrod, 1937).
4. Sonoma flora, Sonoma County: Upper Pliocene (Axelrod, 1944b).

The known records of both *Quercus dispersa* and *Q. douglasoides* in California thus date back at least to transitional Mio-Pliocene time. Axelrod (1944c) points out that the "Southwest American Element" (of which both were presumably members) dominated the lower slopes of the central Sierra Nevada in the early Lower Pliocene. It moved coastward during this stage, and by middle Lower Pliocene had become conspicuous in the coastal region. It may be suggested, therefore, that the existence of *Q. dispersa* and *Q. douglasoides* in the present range of *Q. Alvordiana* could date from this period. In general they may have been more or less isolated ecologically. It seems quite probable, however, that where the woodland association (of which *Q. doublasoides* was an element) adjoined areas of chaparral (of which *Q. dispersa* was an element), ample opportunity for hybridization would have existed.

Apparently no Pleistocene record of any of these three oaks has yet been discovered. One small flora has been recorded, however, from near the eastern base of the Temblor Range in western Kern County (Mason, 1944). The few species recorded suggest an assemblage in which *Quercus Alvordiana* might well have lived. Indeed, the latter is locally abundant today, along the summit of the range to the west.

Certain details of the past history of *Quercus Alvordiana* may be established from geological data (kindly provided by N. L. Taliaferro, Dept. of Geology, University of California, Berkeley; oral communication). Very heterogeneous mixed populations have been noted in several localities which were submerged till very late Tertiary time, e.g., (1) San Emigdio Canyon, Kern County, the type locality of *Q. Alvordiana* (probably submerged until the close of the Pliocene); (2) eleven miles southwest of Coalinga, along Highway 198, Fresno County (submerged until late Pliocene); (3) ca. 4.5 miles south of San Benito, along Highway 25, San Benito County (submerged at least until middle Upper Pliocene). To be sure, mixed populations have been encountered

[4] *Quercus dispersa* has been regarded as a Tertiary equivalent of the modern *Q. dumosa* Nutt., but Axelrod now considers it to be nearer *Q. turbinella* than *Q. dumosa* (written communication, 1948).

in other older areas, but in the case of the populations at the three localities cited there can be no doubt that their development has taken place only since Upper Pliocene time. On the other hand, of the intermediate populations sampled in the present study, those having the greatest apparent homogeneity (Nos. 1900 and 1901: ca. seven miles south of Panoche, San Benito County; fig. 7) occur in an area which has probably been emergent through all of Pliocene time down to the present. Since, as we have seen, the known history of the Tertiary predecessors of both *Q. turbinella* and *Q. Douglasii* goes back well before Upper Pliocene, it is evident, despite the lack of actual fossils of *Q. Alvordiana*, that some populations of the latter have had their development *subsequent* to the (probably widespread) occurrence of the parental species.

Discussion and Conclusions

The principal thesis of this study, that *Quercus Alvordiana* has developed through the interbreeding of *Q. Douglasii* and *Q. turbinella*, seems to be well substantiated by evidence from morphological analyses as well as the field study of leaf persistence. As noted above, paleobotanical evidence is very incomplete, although that available, taken in conjunction with certain geological data, seems to support this hypothesis.

The morphological analyses appear to justify conclusions on several points. (1) In areas where *Quercus Douglasii* and *Q. turbinella* occur in a "pure" state, distant from their region of geographical overlap, they are very distinct from one another. (2) In areas where they occur together in the same general habitat, the common occurrence of forms which are intermediate in varying degrees, furnishes circumstantial evidence of interbreeding. This situation has been encountered in a number of localities including San Emigdio Canyon, the type locality of *Q. Alvordiana*. (3) In populations of either *Quercus Douglasii* or *Q. turbinella*, within or adjacent to the area of overlap, morphological analysis often reveals that some modification exists. The fact that this modification is usually in the direction of the other species is taken as evidence of introgression. (4) Some intermediate populations in the zone of overlap are similar to *Quercus Douglasii*, others are more similar to *Q. turbinella*, and still others are no more similar to one than to the other. This striking morphological diversity must certainly be an expression of extraordinary genetic diversity. Thus *Q. Alvordiana*, together with populations of the parental species modified by introgression, would appear to have a very high potential for further evolutionary development.

Thus *Quercus Alvordiana* is not a homogeneous, clear-cut entity, and just as the living populations present an aspect of considerable complexity, their past history has probably been equally complex. Although no fossils of *Q. Alvordiana* have yet been discovered, certain inferences regarding its past history may be made from other paleobotanical and geological data. Assuming the co-existence of fossil equivalents of *Quercus Douglasii* and *Q. turbinella* in at least some parts of the range of *Q. Alvordiana* as early as middle Lower Pliocene, this opportunity of interbreeding could have resulted in the development of local "hybrid swarms." The trend toward a warmer climate with increasing aridity during the Lower Pliocene, reached its culmination in Middle Pliocene, which in central and southern California was apparently the hottest and driest part of that epoch. Under these circumstances, the semi-arid woodland and chaparral (of which *Quercus douglasoides* and *Q. dispersa* respectively, were components) attained their maximum expansion in central California (Axelrod, 1948). Thus, by Middle Pliocene both of these species could have been rather widely distributed (and frequently sympatric) in central and southern California.

There appears to be general agreement among paleobotanists that the Pliocene was an epoch of diversified topography and climate in California, with strongly localized floristic associations. As a result, somewhat dissimilar types could have been selected out of "hybrid swarms," from place to place, by these diverse environments. Given selection operating over a considerable span of time in each of these environments, plus at least partial geographical isolation, then a diverse series of intermediate populations could have evolved. Shifting climatic conditions of late Pliocene and Pleistocene could have resulted in (1) merging of populations, (2) intrusion of one or the other parental species—which could have further modified such populations—or (3) fresh contacts between the two parents, providing the continuing opportunity for interbreeding that is evidently still occurring at the present time.

Summary

The Blue Oak (*Quercus Douglasii* H. & A.) and Gray Oak (*Q. turbinella* Greene) characteristically occur in quite different ecological associations, although their ranges overlap in the Inner South Coast Ranges (and elsewhere) in central and southern California. Herbarium specimens intermediate in varying degrees between these oaks were observed some years ago. Some of these had been identified as *Q. dumosa* var. *Alvordiana* (*Q. Alvordiana* Eastwood), a problematic entity among Californian oaks—one whose taxonomic status has varied widely with different authors. The postulate was made that *Q. Alvordiana* has arisen through interbreeding between *Q. Douglasii* and *Q. turbinella*.

In order to test this hypothesis, a study was made which included the examination of numerous herbarium specimens, field study, and the analysis of a series of population samples.

The study of herbarium specimens included a survey of the stellate trichomes of the lower leaf surface. It was found that the number of rays per trichome in *Quercus Alvordiana* is more or less intermediate between *Q. Douglasii* (in which 4 is the predominant number) and *Q. turbinella* (in which 8 or more is predominant).

A field study of the relative length of leaf persistence showed that *Quercus Alvordiana* is, in general, intermediate between the deciduous *Q. Douglasii* and the evergreen *Q. turbinella*.

The populations sampled included typical *Quercus Douglasii* and *Q. turbinella*, as well as a number of different populations through the range of *Q. Alvordiana*. These collections were analyzed with the use of a hybrid index, and the data obtained are presented in the form of histograms and pictorialized scatter diagrams. The results indicate that in a number of localities, including the type locality of *Q. Alvordiana* (San Emigdio Canyon, Kern County), *Q. Douglasii* and *Q. turbinella* occur together in the same general habitat with a wide array of intermediate forms. Such intergrading populations have been noted in the inner South Coast Ranges as far north as central San Benito County, on the west side of the Salinas watershed in Monterey County, in the Tehachapi Range, and elsewhere. Throughout the same general area occur more or less intermediate populations which exhibit a combination of the characters of *Q. Douglasii* and *Q. turbinella*.

Direct paleobotanical evidence of the occurrence of *Quercus Alvordiana* in past geological time is lacking, but the known fossil history of *Q. turbinella* [Tertiary equivalent: *Q. dispersa* (Lesquereux) Axelrod] and *Q. Douglasii* (*Q. douglasoides* Axelrod) coupled with geological data, lends support to the writer's hypothesis. The conclusion is drawn that *Q. Alvordiana* has developed through the interbreeding of *Q. Douglasii* and *Q. turbinella*, and an explanation—in keeping with the known geological and paleobotanical facts—is suggested to account for its present heterogeneity.

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THE EVOLUTION OF A PERMIAN VERTEBRATE CHRONOFAUNA

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INTRODUCTION

This paper is concerned with the movement of a complex of interacting vertebrate populations through time under the influence of changing environmental conditions. This complex maintained a basic structural pattern throughout its existence, although, of course, there were changes of some of its components. The maintenance of this structural pattern appears to have been related to the general tendency toward ecological stability of the deltaic environment in which the vertebrates lived. Major changes in equilibrium of the system that might have resulted from immigration tended to be reduced by the partial ecological and geographical isolation provided by the environment, and by the internal balance of the complex, which was strong throughout much of the time involved.

Partial discontinuities exist between ecological systems today and clearly have existed in the past under a wide variety of circumstances. The units thus formed have persisted, changing in varying degrees, but maintaining their fundamental characteristics for periods of time that have geological significance. This persistence is reflected, as in the case studied, in the continuity of the structure of the evolving animal complex that is a part of the total ecological system. At any given moment of time in the history of such a system, the animals properly may be considered to constitute a fauna. The scope of such a fauna is limited by the particular ecological system of which it is a part. Furthermore, for convenience in reference, a fauna may be restricted or qualified, as may be appropriate in a given case, to include only part of the animals, as, for example, in the present case, the vertebrates. Interaction of the animal populations that constitute fauna, either direct or indirect, is implied by the association of the animals, although it is not explicit in the definition of a fauna.

When the factor of duration through time is introduced, the term fauna is no longer strictly applicable and may lead to confusion. For this reason the term chronofauna [1] is proposed to differentiate faunal units in which time is an important factor from those in which it is not. A chronofauna is defined as a geographically restricted, natural assemblage of interacting animal populations that has maintained its basic structure over a geologically significant period of time.

Environment, both biological and physical, plays an important part in most evolutionary studies and interpretations of past environments necessarily are involved in an analysis of a chronofauna. Reconstructions of ancient environments are subject to various difficulties and conclusions are rarely beyond question. Furthermore, there always remain biological and physical factors that cannot be considered. It is possible, nevertheless, to gain information concerning both physical and biological aspects of environment adequate to provide a background for study of many phases of adaptive modifications of animals. Such information becomes especially significant when changes of environment can be related to patterns of stability and modification of the animals of a chronofauna.

Once the history of each species of an assemblage is known and its relationships

[1] This term was suggested by Mr. Bryan Patterson in the course of discussions at an annual meeting of the Society of Vertebrate Paleontology.

to the physical environment have been determined, it becomes possible to interrelate the histories of many species, each of which to a greater or lesser degree provides a part of the environment of others. All known biological and physical aspects of the environment may then be studied in their relationships to patterns of stability and change of the complex of animals. There emerges, when sufficient data are available, a coherent picture of the evolution of a chronofauna in which the course of evolution of the elements, the populations, takes on new meaning in terms of the whole.

The Permian assemblages considered in the following sections of this paper constitute a vertebrate chronofauna. Interpretations of these assemblages and their environments are based upon information accumulated during some 17 years of study of the fossils and their field relationships. The animals are distributed among fish, amphibians and reptiles, the time is Early Permian and the physical setting was a delta. The delta lay marginal to non-deltaic areas, from which immigrations of vertebrates took place to modify the deltaic assemblage to a degree noted later in this report.

The Permian Chronofauna and Its Environment

The Geographic and Geologic Setting

The map[2] (fig. 1) shows the area of north central Texas with which the study is concerned and certain gross features of the geology. The vertebrates have been collected from the Arroyo, Vale and Choza, successively younger formations of the Clear Fork group of Early Permian age. Somewhat similar assemblages are well known from the underlying formations of the Wichita group, but the discussions will be limited to the formations cited above. The beds strike NE–SW and dip approximately 50 feet per mile to the northwest. The section is about 2,200 feet thick and the time involved in deposition probably was somewhere between 3 and 10 million years, perhaps nearer the former than the latter.

Certain major environmental features of this area during the Early Permian are fairly evident. The sediments were deposited on a delta that was margined by the sea to the south and west and by land to the north and east. The delta appears to have been sufficiently limited so that climatic differences between one part and another would not have been great. The sea did not cover the area during the Clear Fork, although it had done so earlier in the Permian and transgressed again later. Temperatures appear to have been moderate, for the animals and plants could not have otherwise survived. Rainfall was sufficient to support ferns, seed ferns, equisitales and conifers as well as to supply streams and ponds in which various fish and amphibians lived. The climate may be roughly compared to that of the same area in north central Texas today with, apparently, less seasonality and greater rainfall during the early part of Clear Fork time.

Study of more subtle aspects of the environment and the changes that occurred with time entail detailed analyses of intricately interrelated physical and biological evidence. Space permits only a summary statement of conclusions. Four principal physical subzones, which provided habitats for vertebrate animals, may be recognized: streams, ponds and lakes (hereafter referred to as ponds), pond margins, and flood plains and divides. The last mentioned will be referred to as uplands for the sake of simplicity. These subzones are not, of course, to be considered as completely separate units, for each makes marginal contact with the others and animals certainly would have tended to pass beyond the limits of a single subzone. Rather, they should be thought of as the principal, but not necessarily limiting, habitats of the various animals.

[2] This map is reproduced from Olson (1951a, fig. 1) with permission of the University of Chicago Press.

Each of the subzones can be recognized in the field from physical criteria. These include both gross features of the sedimentary deposits such as attitudes of beds, lateral continuity, etc., and internal characteristics of beds such as the size and arrangement of grains and composition. Pond deposits, for example, are characterized by gently dipping marginal beds, generally ovoid or elliptical outline, small size of particles and uniformity of particle size in a given bed, as well as color differences from surrounding sediments that reflect, in part, compositional differences. Deposits laid down in other subzones have equally distinctive features.

A brief survey of the environmental changes during the Clear Fork is given in figure 2. The sedimentation in the Arroyo was dominantly on flood plains. A thin but extensive series of red shales, silts and sands, deposited near the end of the Arroyo, indicates a marked change in environment. These deposits appear to have been laid down when the delta was extremely low. Of the four subzones, only the ponds appear to have remained habitable during this time. It is probable

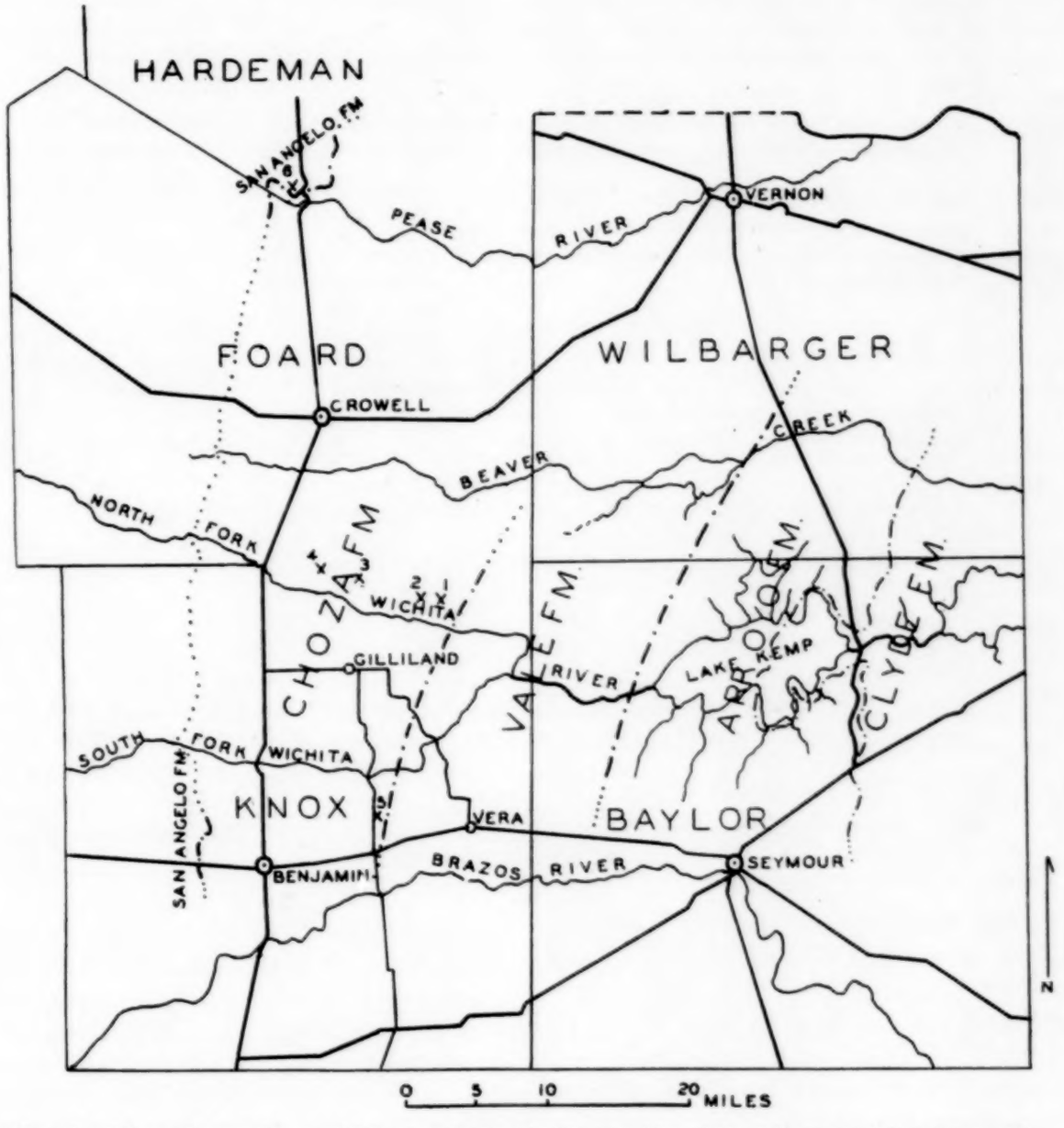

FIG. 1. Map of area from which vertebrate fossils considered in this paper have been collected. The approximate positions of formational boundaries are indicated on the map.

FM	Sedimentation	Topography	Rainfall
2200′	Extensive, even clay, sand and evaporite beds. Few channels and ponds. No known life record.	Same	Low rainfall
Choza	Predominantly flood plains. Channels small, few, widely spaced. Evaporite basins markedly increased. Some Playa, fresh water ponds.	Local relief low. Land near sea level.	Continued decrease in total rainfall.
	Few channels, not clay-pebble type. Initiation of evaporite beds. Scattered fresh water ponds.	Local relief moderately low. Basins with fresh water and evaporite deposits.	Decrease in total. Not torrential. Seasonality persistent.
1200′	Channel and lag deposits all of clay-pebble conglomerates, sediment locally derived. Ponds scattered, predominantly persistent. Ponds show seasonality in nature of deposition.	Local relief increased.	"Monsoonal" type fully developed. Torrential seasonal rains.
	Same, but beginning of clay-pebble conglomerates, derived from local sediments.	Local relief same. Source area high.	Initiation of "Monsoonal" type.
Vale	Marked channel development. Coarse, dipping, marginal flood plain deposits. Few but extensive ponds. Coarse materials of streams derived from source area.	Moderate local relief. Marked increase in relief in source area of sediments.	Increase in seasonality in source area of streams.
	Initiation of large stream channels with conglomeratic deposits. Ponds widely spaced.		
700′	Even red shale, with broad linear belts of silt and fine sand. Deposited by very slowly flowing water. No definite channels and few ponds.	Local relief very low. Area near sea level. Possibly tidewater estuaries.	Same.
Arroyo	Slight increase in ponding, especially temporary ponds.	Same	Slight increase in seasonality.
	Flood plain deposits predominant, a few scattered ponds. Divides low, streams small.	Local relief low. Source area of streams low.	Moderate, evenly distributed throughout year.

FIG. 2. Chart of environmental conditions during the Clear Fork. The thicknesses of formations are only approximate.

that the water courses became somewhat saline as a result of tidal effects. Local relief appears to have been low both in the delta and on adjacent land during the Arroyo. Rainfall appears to have been moderate and rather evenly distributed throughout the year.

The Vale was marked by a rapid increase in development of major stream channels, as indicated by deposits of conglomerate and coarse, dipping marginal flood plain deposits. Clay-pebble conglomerates became dominant in the upper half. Relief appears to have increased markedly, first in the non-deltaic areas and then on the delta. Sedimentation

suggests that seasonality of rainfall increased, with eventual establishment of monsoonal conditions.

The Choza opened with rapidly decreasing local relief and by mid-Choza the surface of the delta lay near to sea level. Rainfall decreased, with seasonality persisting, to produce rather arid conditions accompanied by development of evaporite basins. Such basins are formed where deposition of salts takes place from waters that have become highly saline through evaporation.

The Chronofauna and Its Subzonal Assemblages

The chronofauna considered in the analyses that follow includes genera and species for which information on identity, frequency, and distribution is sufficient to be meaningful. Vertebrates not specifically considered certainly played a part in some of the changes witnessed, but it is impossible to evaluate their importance. Twenty-one genera and thirty-two species of fish, amphibians and reptiles are included. The genera are listed in figure 3 along with stratigraphic data for each. Environmental distributions and the habits of the animals are more important in the present considerations than classification of the genera into appropriate higher categories, and the latter will not figure prominently in the discussions.

Fish are represented by a fresh water, predaceous shark, and by lung fish. It is certain that many of the waters were inhabited by small fish, probably palaeoniscoids for the most part, and that these fish formed an important part of the diet of other water living animals. Both labyrinthodont and lepospondylous amphibians figure prominently in the fauna. Reptiles are all relatively primitive types, being distributed among the Seymouriamorpha, Diadectomorpha, Captorhinomorpha, and Pelycosauria. Only passing reference will be made to the plants, which have a fair fossil record, and invertebrates, which have almost no record. It is not to be supposed, however, that they are not considered important in the evolution of the vertebrates.

The problem of analysis of the interrelationships of the species in the various environmental subzones and between subzones is intricate. As a first step in analysis, the assemblage of each subzone will be examined without reference to environmental interrelationships.

Upland Subzone. This subzone, alone among the four, is thought to have continued with little change into the land areas adjacent to the delta. It is believed, furthermore, that the inhabitants occupied the subzone, insofar as their particular niches were available, throughout its geographic extent. Genera known from equivalent deposits in Oklahoma tend to support this conclusion. The most important points concerning this subzone are as follows:

1. *Dimetrodon gigashomogenes* is present in the Arroyo, Vale, and lower and middle Choza. *Captorhinus aguti* occurs from the base of the Arroyo through the upper Vale. There are traces of the genus in the lower and middle Choza, but remains are so fragmentary that species determination is uncertain. No differences from *Captorhinus aguti* have been noted and the specimens have been tentatively referred to this species. The only break in stratigraphic continuity of *Dimetrodon gigashomogenes* and *Captorhinus aguti* is at the red shale zone at the top of the Arroyo.

2. Two species, *Dimetrodon major* and *Diadectes tenuitectus*, disappear by the end of the Arroyo, both diminishing in numbers prior to their disappearance.

3. A new, larger species of *Captorhinus* (possibly a new genus) unnamed as yet, appears in the Vale in the same subzone as *Captorhinus aguti*. It is probable, on the basis of size and dentition, that the dietary habits of the two were somewhat different. This species has not been found in the Choza.

4. *Casea broilii* appears in the record at the beginning of the Vale. Two spe-

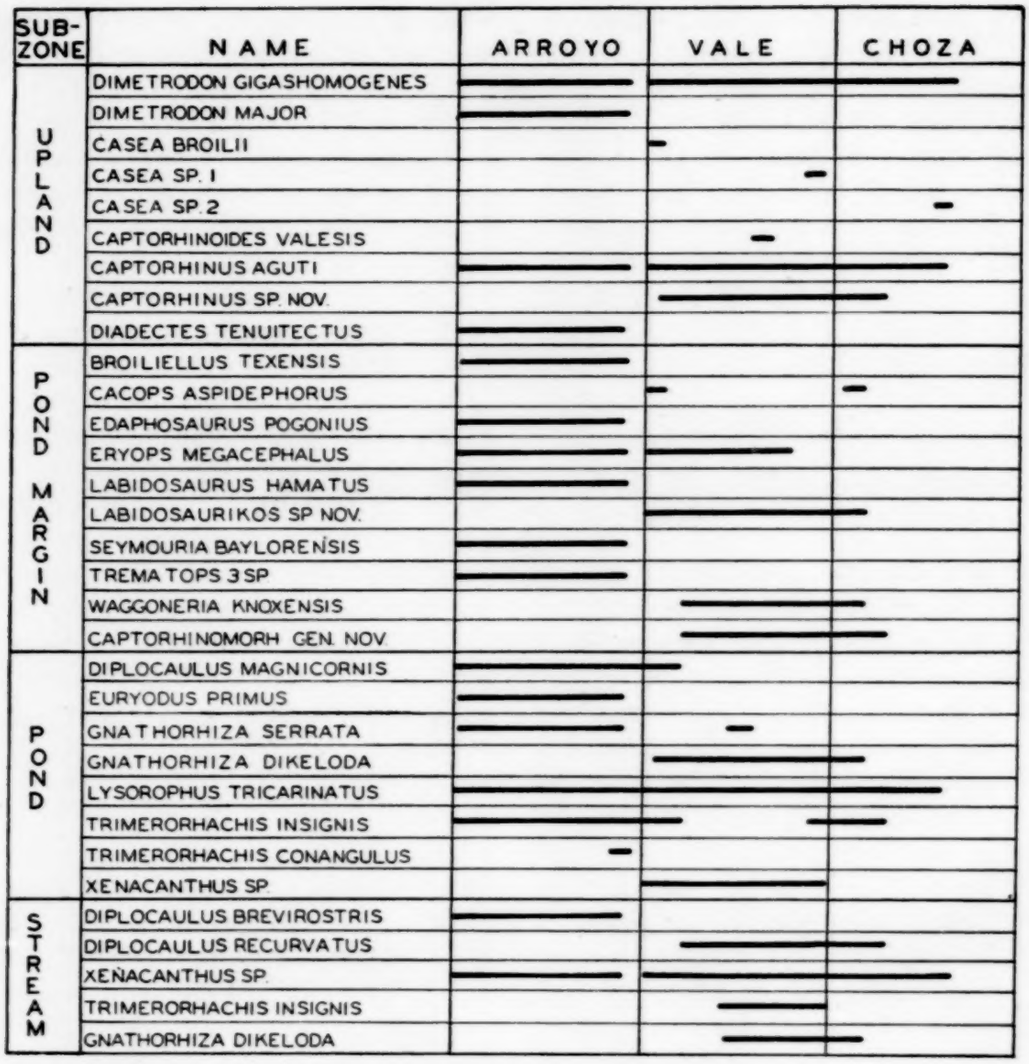

FIG. 3. Stratigraphic and subzonal distribution of genera and species of vertebrates during the Clear Fork.

ies, successively larger, are found, one in the upper Vale and the other in mid-Choza.

Pond Margins. This environmental subzone is believed to have been largely, if not entirely, restricted to the delta. The following points are of particular importance:

1. Only one Arroyo species, *Eryops megacephalus,* persisted into the Vale. It appears to have diminished greatly in numbers from the mid-Arroyo on, and is unknown above the base of the upper Vale. Two species of captorhinomorph reptiles, one seymouriamorph and one dissorophid amphibian appear in the subzone during the lower Vale.

Ponds. Ponds and lakes of the types encountered are not known to have existed beyond the limits of the delta. The following items are of especial significance.

1. The pond species that persisted into the upper part of the Arroyo consistently passed the Arroyo-Vale boundary without change.

2. These species failed to persist in the pond environment, except the burrower, *Lysorophus tricarinatus,* beyond the lower part of the middle Vale.

3. *Trimerorhachis insignis* reappeared in the upper Vale in the ponds. It is not known to have been associated with *Xenacanthus* at this level.

4. *Xenacanthus,* a predaceous shark, is found in ponds in the lowest Vale. It is associated with *Diplocaulus magnicornis* and *Trimerorhachis insignis,* aquatic amphibians. It persisted in this environment until the upper Vale, but it is not present in all of fossiliferous pond deposits of that time. It has not been found in ponds of Choza age, although it is common in the stream deposits.

5. A large species of lung fish, *Gnathorhiza dikeloda,* appeared in pond deposits shortly after the beginning of the Vale. It seems to have been derived from

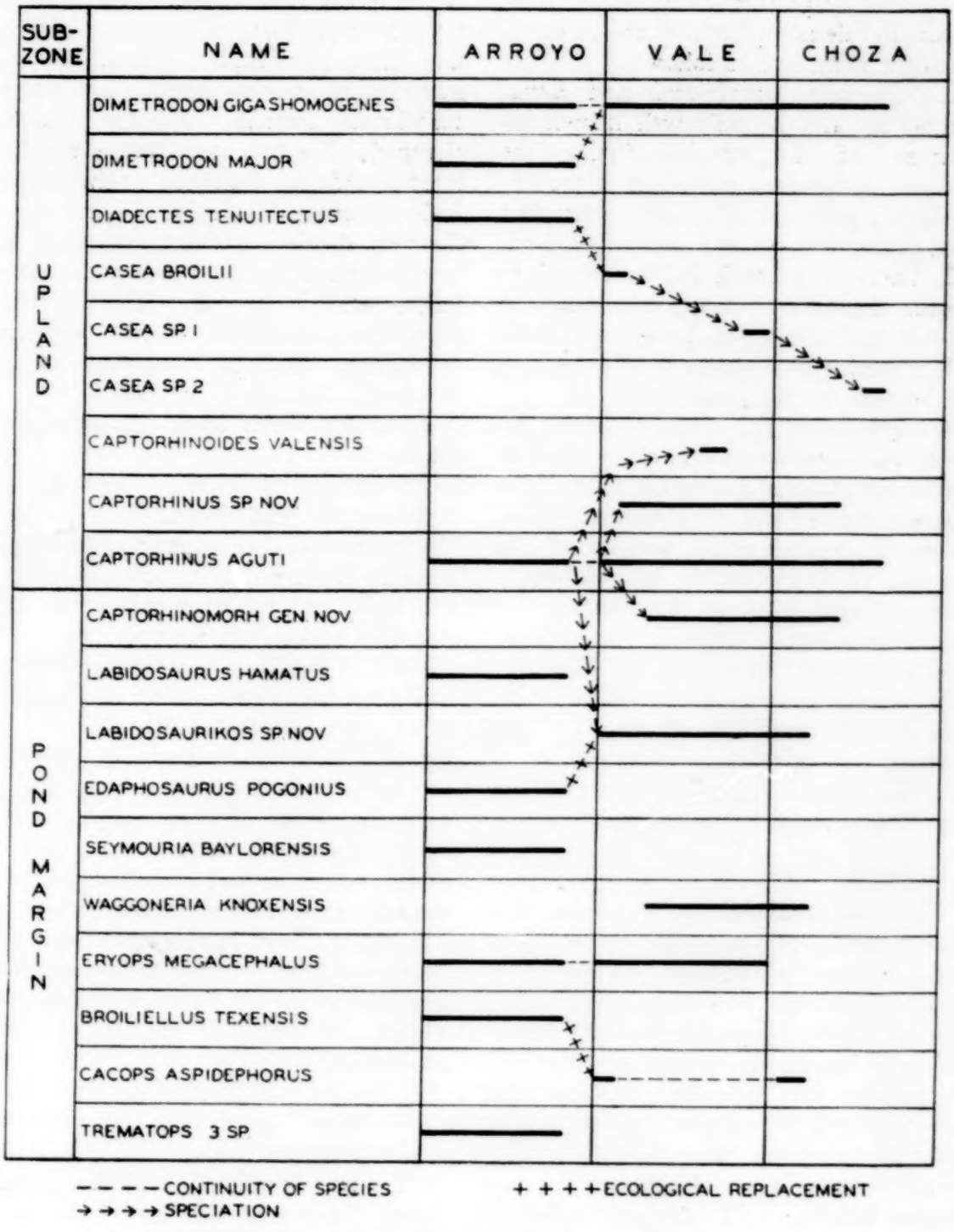

FIG. 4. The genera and species of the upland and pond margin subzones showing the histories and interrelationships during the Clear Fork.

Gnathorhiza serrata, and to have coexisted with this species until the beginning of the upper Vale.

Streams. Although there is no doubt that the streams of the delta were fed by those of adjacent, higher lands, the fate of the species inhabiting the deltaic streams strongly suggests that there were no effective migrations between the nondeltaic and deltaic phases of the streams. Pertinent items are as follows:

1. *Diplocaulus brevirostris* and *Xenacanthus* sp. are the only well known inhabitants of the streams during the Arroyo. Coprolites of the latter contain scales of paleoniscoids, indicating that these small fish were a source of food.

2. There is a break in the record of stream deposition during the time of deposition of the upper Arroyo red shale.

3. *Diplocaulus brevirostris* did not persist beyond the red shale zone.

4. *Diplocaulus* sp., *Trimerorhachis insignis* and *Gnathorhiza dikeloda* came to inhabit the streams during the Vale. The first was derived from *Diplocaulus magnicornis,* a typical pond animal of the Arroyo. *Trimerorhachis insignis* was a common pond form in the Arroyo, not known from stream deposits. It is abundant in stream deposits in the Vale and very rare in ponds. *Gnathorhiza dikeloda,* derived from a pond species of the Arroyo, was successful in the streams of the Vale and *Xenacanthus* continued to be present in the streams in large numbers.

Interpretation of the Evidence

The most vital part of the basic data upon which analyses of the evolution of the vertebrate assemblages of the delta may be based has now been briefly summarized in the figures and text. To reduce the complexities that are involved in treating the different subzones and their changing occupants together, analyses will be made by citing, and illustrating by examples, a series of points under two general headings: (I) the persistence of species, and II patterns of modification.

I. The persistence of species:

1. In the same subzone during a period of time that witnessed changes both in physical and biological factors of environment.

Dimetrodon gigashomogenes and *Captorhinus aguti,* both of the upland subzone, illustrate this pattern (fig. 4). They both persisted from the beginning of the Arroyo into the Choza without detectable morphological change. During this time, topography, rainfall, both in amount and seasonal distribution, and the associated animals of the subzone changed. The two species appear to have lived outside the delta during the Arroyo-Vale transition. In spite of these events, the two species persisted and their success is attested by the relative abundance, particularly in the case of *Dimetrodon gigashomogenes,* in rocks deposited throughout much of the period of time involved.

2. In transition from one subzone to another.

Persistence of species under this circumstance is best illustrated by *Trimerorhachis insignis,* an aquatic amphibian, in its shift from ponds to streams early in the Vale and its reappearance in large numbers in ponds in the upper part of the formation (fig. 5). *Gnathorhiza dikeloda* and probably *Xenacanthus* sp. represent other cases. Both stratigraphic and biological evidence concerning *Trimerorhachis insignis* has been derived from an extensive series of observations. Statistical analyses of reasonable samples of skulls, vertebrae and limb bones have revealed no significant differences in the animals involved in the transitions cited. Whatever changes may have occurred in physiology or soft anatomy without affecting the osteology cannot, of course, be determined.

3. In a special, limited environment.

The highly specialized, elongated, burrowing, aquatic amphibian, *Lysorophus tricarinatus* persisted without apparent change from near the base of the Arroyo through the lower one-third of the Choza (fig. 4). It is abundant throughout, sug-

gesting consistently large populations. It lived, during this time, in ponds, most of which appear to have been dry during part of the year. Specimens are found coiled and in concentrations in most instances, suggesting that many died while in burrows. Although association with other species is uncommon, uncoiled specimens have been found in pond clays along with other aquatic vertebrates. Presumably these met death during non-aestivating phases of their existence. Apparently the associated forms, different at various times during the Clear Fork, did not exercise selection pressure sufficient to initiate any evolutionary changes in *Lysorophus tricarinatus*.

II. Patterns of modification:

1. Phyletic evolution of a species in a single environmental subzone.

Evidence for this type of change is found in the rather meager remains of the genus *Casea* (fig. 4). The three species, lower Vale, upper Vale, and mid-Choza, respectively, show rapid increase in size, and accompanying proportional modifications of various skeletal parts. There appears to be a drift toward larger size, probably through selection of larger members of successive populations. *Casea* was herbivorous and size increase was, perhaps, related to the advantage that size would give in warding off the attacks of carnivores. It is interesting to

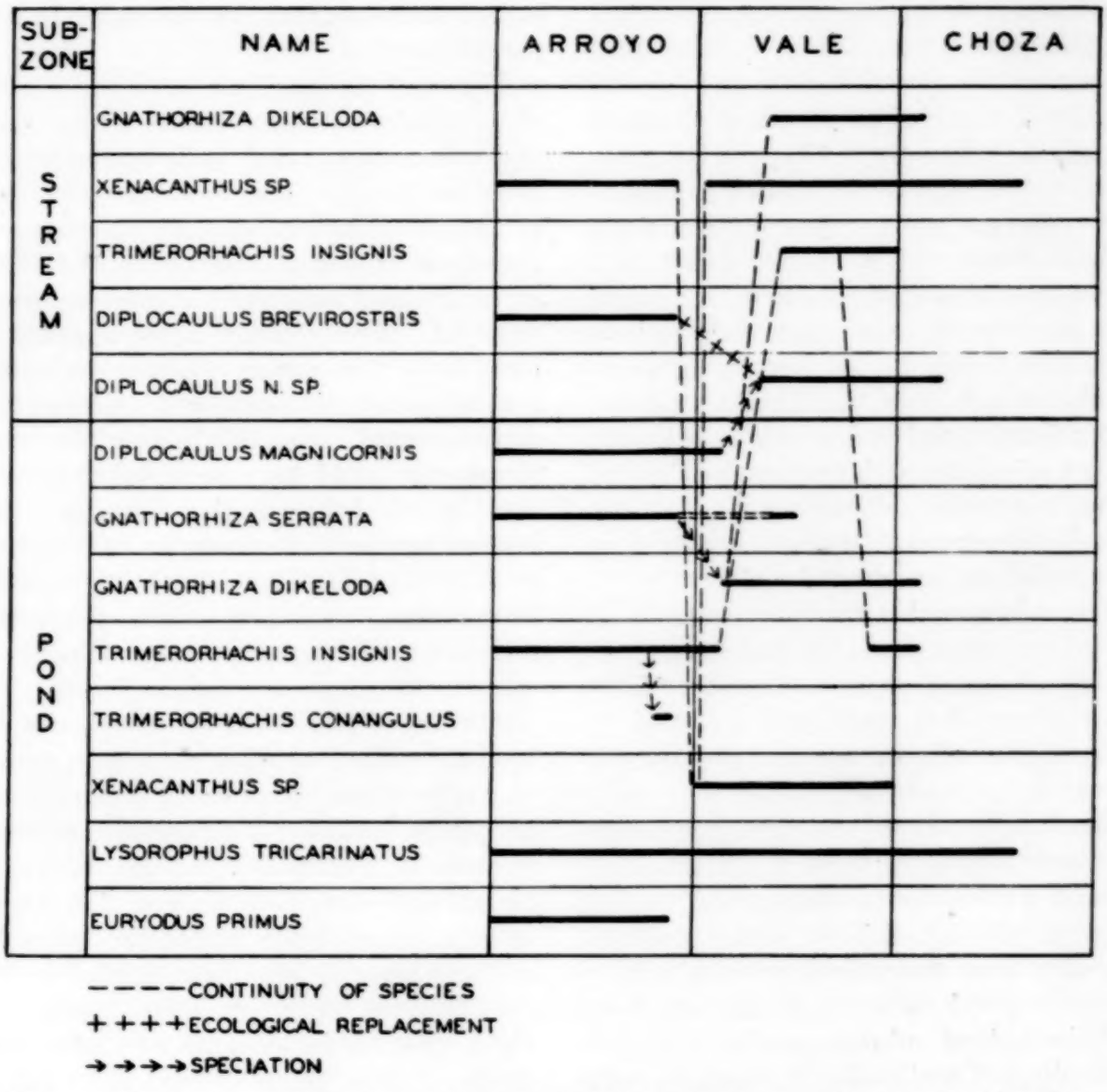

FIG. 5. The genera and species of the stream and pond subzones showing the histories and interrelationships during the Clear Fork.

note that there is no commensurate increase of size in the principal large predator of the upland zone, *Dimetrodon gigashomogenes.*

2. Numerical decrease and final disappearance of species during a period of time marked by no recognizable pronounced change in biological or physical environment.

This pattern is not infrequent in paleontological studies. It is best shown in the fauna under consideration by *Diadectes tenuitectus* (fig. 4). There is no evidence that the diminution in numbers and extinction were dependent upon outside physical or biological factors. If this is accepted as showing that there were, in fact, no external influences, the decrease in numbers and extinction must have resulted from internal factors. This is, of course, not out of the question and such factors have been appealed to in many instances to explain extinctions. There is, however, considerable danger in drawing conclusions from such negative evidence, especially in cases such as this in which it is inevitable that various factors that might have been operative are not likely to have left a clear record. At present it seems possible only to note that *Diadectes tenuitectus* disappeared and, so far as is known did not reappear, with reasons for the presumed extinction unknown.

3. Environmental change resulting in unoccupied environmental niches.

The evidence that this phenomenon occurred is drawn primarily from events affecting the pond margin subzone. With onset of very low lands at the end of the Arroyo, this subzone appears to have disappeared. Obviously, since the ponds themselves continued to exist, pond margins were physically present. Their existence as a life subzone comparable to that existing during the Arroyo, however, probably was dependent upon a balance with the pond subzone on the one hand and the upland subzone on the other, for both physical and biological features were somewhat transitional. With the disappearance of the upland subzone, this balance was destroyed, and, it would appear, the pond margins were unable to support the type of organisms that had previously found them suitable. Temporarily, thus, this subzone and its niches became impoverished. The failure of the species of the subzone to reappear when the habitat was reestablished in the lower Vale indicates that no refuge areas existed beyond the limits of the delta; that is, the subzone was confined to the delta. Thus, when the subzone did reappear, it offered open ecological niches. The same applies, in part, to the other subzones but the pattern of occupancy tends to be less clear. The series of events just described is related to points 4 and 5 considered below.

4. Speciation related to occupancy of niches and subzones not occupied by the parent species.

This and the next point concern modes of occupancy of vacant niches in the various subzones, created as indicated in the previous point. The most striking case is the development of new species and genera of captorhinomorph reptiles both in the upland and pond margin subzones (fig. 4). *Captorhinus aguti* appears to have been the source of this radiation, but, of course, this cannot be conclusively demonstrated. On the basis of its morphology it could have occupied this position, something not true of any other known species. Temporally it is appropriately placed. The assumption is therefore made that it represents the actual ancestor. Changes were principally in size, proportions of skeletal parts, and dentition. Within the subzone occupied by *Captorhinus aguti* arose a new species of *Captorhinus,* or possibly a new genus, as yet unnamed. Presumably isolation related to occupancy of an ecological niche, different from that of the parent species, occurred, and the principal changes seem to have been related to diet. Adults were about one-third larger than the largest adults assigned to *Captorhinus aguti.* A new genus in the same subzone, *Captorhinoides valensis,* differs from *Captorhinus,* most importantly, in audi-

tory structure (Olson, 1951a). The adaptive significance of this change is obscure. Two genera, *Labidosaurikos* and an unnamed genus, developed in this radiation, invaded the pond margins in the lower Vale, occupying the niches left open by the depletion of the Arroyo occupants, and became fairly abundant in this subzone by mid-Vale. Both are characterized by highly modified dentitions, derivable from the *Captorhinus* pattern, and moderately large size. Both appear to have been herbivores.

This radiation occurred during a short period of time. Intermediate stages between *Captorhinus aguti* and the genera and species believed to have been derived from it are not certainly known.

5. Occupancy of ecological niches of a subzone, impoverished by temporary change and then re-established, by species unable to penetrate the delta when the subzone was inhabited.

This appears to have occurred in a number of instances in which animals that had lived in non-deltaic areas found suitable habitats in niches of the delta that developed after the time of the deposition of the red shale near the end of the Arroyo (figs. 4 and 5). Such animals were not, so far as known, derived from species existing on the delta during the Arroyo, and it is thus inferred that they, or their ancestors, lived elsewhere, presumably in the higher lands away from the delta. *Waggoneria,* a seymouriamorph, *Cacops,* a dissorphid amphibian, and *Casea,* a pelycosaur, are examples. This phenomenon has not been recognized in the stream or pond habitats, probably because of the almost immediate occupancy of the environment by predaceous sharks in the first instance and the persistence of the habitat across the Vale-Arroyo boundary in the second.

6. Modifications of faunules, migrations, and speciation related to occupancy of a subzone by a species not previously represented.

This point concerns a rather complex series of events and involves an intimate knowledge of a complex and its physical environment for interpretation. For illustration, one such series pertaining to the ponds and streams will be summarized (fig. 5).. *Xenacanthus,* the predaceous shark, inhabited streams but is unknown from the ponds during the Arroyo. It appeared in the ponds in the lowest part of the Vale. This transition is thought to have resulted from the pressure exerted by the virtual disappearance of the stream habitat, perhaps as a result of tidal penetration, during the red shale interval. During the Arroyo, *Xenacanthus,* was associated with *Diplocaulus brevirostris,* a stream-dwelling species of aquatic amphibian, but not with *Diphocaulus magnicornis* or *Trimerorhachis insignis,* Arroyo pond dwellers. *Diplocaulus brevirostris* disappeared during the deposition of the red shale and did not reappear. *Xenacanthus,* on the other hand, is found in lower Vale pond deposits in association with *Diplocaulus magnicornis, Trimerorhachis insignis,* and the lung fish, *Gnathorhiza dikeloda.* Soon after this association had been realized, *Diplocaulus* and *Trimerorhachis* disappeared from ponds only to appear in the streams. It is believed that these amphibians were unable to persist in the quiet pond waters in association with the predaceous shark, but were able to meet this competition in the streams. *Trimerorhachis* shows no change in the course of transition but *Diplocaulus* is represented by a new species in the streams.

The "horns" of the somewhat triangular skull of *Diplocaulus* are strongly recurved in the new species, a character that may be called "crook" for ease of reference. In this character, the skulls of the new species somewhat resemble those of the stream species of the Arroyo, *Diplocaulus brevirostris.* All other characters of the skull, however, resemble those of the pond species of the Arroyo, *Diplocaulus magnicornis,* very closely, so that there can be no doubt that this was the source of the new species (Olson, in press). The character of crook does

occur in *Diplocaulus magnicornis* with a frequency of 16 in 100 (based on a sample of 50). Field evidence indicates that this character was randomly distributed throughout the population both in space, at any particular time, and during the time through which the species is known to have existed, i.e., the time represented by the deposition of the Arroyo formation. The distribution of crook and straight "horn" in the sample of *Diplocaulus magnicornis* is suggestive of a morphological expression of equilibrium attained under conditions expressed by the Hardy-Weinberg law.[3] It seems probable that population size and changing environmental conditions, offering some selective advantage, would have vitiated complete conformity to this principle. In spite of these factors, the equilibrium concept is valuable in an interpretation of the population structure as it has been observed.

The character of crook is present in all known specimens of the new species of *Diplocaulus* from the Vale in which the postero-lateral part of the skull is preserved (about 20 individuals). The presence of this character in *Diplocaulus magnicornis* gives, in one sense, a partial preadaptation to stream life. It appears that the members of the population of *Diplocaulus magnicornis* that possessed this character were the source of the new species. They had the ability to penetrate streams, and thus to become isolated during a time when existence of the genus in the ponds became precarious and eventually impossible.

Whereas the two amphibians left the pond environment, the lung fish, *Gnathorhiza,* seems to have met the onslaught of *Xenacanthus* successfully. It is possible that *Gnathorhiza,* presumably a bottom feeder, did not come into direct competition with *Xenacanthus.* The Arroyo species of *Gnathorhiza, G. serrata,* which is rare throughout the Arroyo, is known to have crossed the Arroyo-Vale boundary, for it occurs in the middle Vale. It has been found in pond deposits. In the lower Vale, another species, *G. dikeloda,* larger in size and with more highly developed sectorial teeth, appeared in the ponds (Olson, 1951b). It is thought to have arisen from *Gnathorhiza serrata,* the only possible known source, but intermediates have not as yet been identified. This appears to be a case of speciation induced by the introduction of a new predator in which marginal survival of the old species continued while the new species not only thrived in the initial subzone, presumably in a different ecological niche, but was able to penetrate a new subzone, the streams.

7. Interdependence of faunules of two or more subzones.

No doubt such relationships existed in a complex fashion between all adjacent subzones and their various subdivisions. Only one of several known instances in the Clear Fork will be cited to illustrate the part that this interdependence may play in the evolution of the chronofauna (fig. 5). It has been noted that the assemblage of the pond margins of the Arroyo was composed, in large part, of carnivores, *Edaphosaurus,* being the exception. The food source must have been in part the animals of the ponds. It has also been shown that, shortly after the beginning of the Vale, the pond assemblages changed markedly with the result that potential prey for marginal predators was greatly reduced. The captorhinomorph radiation and immigrations that took place early during deposition of the Vale, repopulating the pond margins, produced a great preponderance of herbivores. The only known carnivores are *Eryops megacephalus,* a species that persisted from the Arroyo, and *Cacops,* an amphibian adaptively very similar to *Broiliellus.* Both are low in frequency of occurrence. It seems justifiable to infer a causal relationship between the reduction of potential prey in the ponds and the preponderance of herbivores in the newly developed faunule of the pond

[3] See Stern (1943) for a brief exposition of this concept.

margins. This chain of events and reasoning may be carried further to include the effects of the change of the marginal animals on those of the upland, for again there is a predator-prey relationship, and to the part that this played in modifications of the assemblage of the streams. What has been said, however, will be sufficient to indicate the type of evidence that is available and one instance in which an interpretation has been made.

8. Disappearance of a chronofauna with gradual but intense changes in physical environment.

Heretofore, attention has been directed to patterns of change that did not alter the basic characteristics of the chronofauna, cases in which physical changes were not sufficient to have drastic effects. The present case is the story of the Choza, the last page in the history of the Clear Fork chronofauna on the delta. Physical changes were primarily a continued lowering of the land and decrease of rainfall to the point of incipient aridity. Fossil remains tend to occur increasingly in local concentrations, either in deposits laid down in streams or ponds. The number of ecological niches available to vertebrate life appears to have been successively reduced, with elimination of some species and intense competition between those whose niches persisted. Changes appear to have been such that for the most part they could not be met by speciation; in only one line, that of *Casea,* does a new species appear. This represents continuation of a tendency toward larger size initiated earlier. The only other evidence of change is the appearance of a new eryopid amphibian of somewhat uncertain affinities. Thus, under changes that exceeded the tolerance of many species, there seems to have been extinction rather than modification to meet the changes. In the mid-Choza, all known specimens of animals and plants have come from ponds, their margins, and deposits of small channels leading into these ponds. Only a few such deposits are known in the upper one-third of the Choza and they are unfossiliferous. To the best of our knowledge the vertebrates had gone from the delta. It seems improbable that those elements that were strictly deltaic in habitat left direct descendants, unless it were possible for them to invade the non-deltaic areas either with or without change. The events noted at the Arroyo-Vale boundary suggests that this would have been improbable in most cases.

The only later vertebrate fauna known from the Permian of North America comes from the San Angelo formation that overlies the Clear Fork disconformably. As yet this recently obtained fauna has not been studied in detail. No trace of any Clear Fork genus, except *Xenacanthus,* has been encountered.

Conclusions

What follows is an attempt to generalize from the specific problems considered previously. An element of speculation, of course, enters in since the data are incomplete. The generalizations concern patterns of interaction within a chronofauna. To establish the position of this level, I will allude briefly to a discussion by Dobzhansky (1941, pp. 152–154) in "Genetics and the Origin of Species" in which he differentiates the factors active at two levels of organization: the physicochemical principles involved in the origin of variation and the principles of physiology of populations at the population level of organization. The basis of the present study, is an extension to a third, or ecological level, that of the chronofauna involving the interaction of populations. The behavior of individual populations is injected into this field of action, but basic factors are different from those concerned exclusively with populations. Certain of these factors are outlined and discussed in "Principles of Animal Ecology" by Allee, Emerson, Park, Park, and Schmidt (1949).

It has been shown that various species had different histories during the time represented by the Clear Fork. The

course followed by each is the function of a complex series of variables, some of which can be recognized and evaluated, as noted in the preceding sections, others that can only be surmized and some, undoubtedly, that remain undetected. Most important is the point of view that all species are interrelated and that the constitution of the complex of animals at any given moment is the resultant of the patterns of interrelationship. This concept introduces additional variables that relate to interdependence and interactions of populations, particularly as they modify the significance of such items as population size, variability of species, ecological niches, environmental subzones, etc., in contrast to the way that they are usually viewed when single populations are considered.

In the preceding paragraphs an effort was made to interpret interactions of species and their environments whenever they could be related to positive events. From these interpretations we may now attempt a synthesis. Points that seem to derive from observations and interpretations that have been made are as follows:

1. A chronofauna tends to remain virtually unchanged as long as environmental conditions, or possibly factors of population structure unrelated to environment, are not modified sufficiently to result in the elimination of one or more of its component species. Such identity may be preserved in the face of changes that enlarge or restrict ecological niches and thus affect the population size of the occupying species. Minor changes in species may occur through phyletic change of a population within a particular niche without isolation or significant change in variability (see point 5 below).

2. Environmental changes that occur over a relatively short span of time may tend to result in modifications of structure through:

(1) Alteration of faunal balance by elimination of one or more species, rather than by initiation of adaptive modification within those populations whose niches are affected.

(2) Initiation of change in habitat of the part of a population that may be preadapted to another available habitat:

(a) The affected part may be virtually the whole population, in which event the shift may be made without marked morphological or physiological change or modification of variability (see for example, *Trimerorhachis insignis*, p. 10).

(b) It may involve only a fraction of the total population, the part that is morphologically preadapted (for example, the presence of Crook in 16 per cent of the sample of *Diplocaulus magnicornis*, see p. 14). In this event, the shift involves selection and reduction of variability. This can be recognized in fossil vertebrates only if selection involves osteological features.

3. Open ecological niches may be established through physical changes as follows: the niches, and their inhabitants, that exist when physical change begins, are destroyed as a result of the change. Re-establishment of physical conditions not greatly different from those that existed at the onset of change tends to result in re-establishment of potentially similar, but unoccupied niches. Such re-established niches tend to be filled rapidly by speciation of members of the chronofauna and immigration from adjacent environmental subzones. Re-establishment of balance can produce moderate changes in a chronofauna over a very short span of time.

4. Entrance of a new species into an environment, such as a subzone, occurs only:

(1) When an ecological niche is open, or:
(2) When a niche is very inefficiently occupied with respect to the usurper's potential.

Such an occurrence may disrupt the balance within a subzone. Through this avenue, the total balance may be affected sufficiently that considerable reorganization takes place within a chronofauna.

5. Phyletic change of the occupant of a particular ecological niche may occur when all niches of a subzone are occupied, as long as adaptation to the specific niche alone is perfected, without materially altering other parts of the chronofauna. Such change need involve neither isolation nor reduction of variability. Successive stages in a phyletic series, viewed discretely, correspond in all respects to species, as, for example, in the genus *Casea,* p. 11. In this sense phyletic change involves speciation. The mode of initiation of change, however, may be different from that in which virtually nontemporal isolation of parts of a single population occurs and initiation of change is directly related to this isolation.

Within these five points lie the principal factors of modification of a chronofauna that have been witnessed in the current study. Stability under the influence of slow and moderate physical change stands out. Evolution may occur under such circumstances but seems to have little effect upon internal balance. It can become important if it contributes to a significant modification of the environment of other populations, either by direct invasion of ecological niches or by indirect impingement upon the niches. This has not appeared as an important factor in the problem studied.

The elimination of parts of a chronofauna through environmental change and subsequent speciation or immigration by new or remaining elements into new and/or re-established subzones and niches are the most important factors in the modification of a chronofauna. Evolution of populations through successive small changes (that may tend toward adaptations to new circumstances as they arise) appear to have only a minor effect upon equilibrium. An extinction or migration of one or more species, which may result from a change in the environment that is inconsequential in its direct effect on most species can be effective in establishing a lack of balance and in producing subsequent drastic changes as equilibrium is re-established. When such an event occurs at a time when changing conditions are tending to produce an environment that approaches the limits of tolerance of an appreciable number of species, extinction of much or all of the chronofauna is a probable result. This probability follows logically from the concept of interdependency of species and the apparent inability of many species to adapt to extensive change over a short period of time. The events of the Choza discussed earlier in this paper provide illustration of this series of events.

It is tempting to speculate beyond the limits of this case and to suggest that widespread physical change, as appears to have occurred at various times in the geological history of the earth, might initiate loss of equilibrium over widespread areas. Extinction of many species would be expected as chains of interrelationships were destroyed by the loss of a few. Most likely to succeed under these circumstances and to provide a basis for re-establishment of equilibrium would be those populations that in one way or another were preadapted to circumstances not dependent upon the particular linkages with which these organisms previously had been associated. There would result new chronofaunas, very different from those that existed prior to the initiation of the changes.

Summary

An analysis of the interrelated changes of the species of a chronofauna with time and altering environmental conditions has been based upon studies of an Early

Permian fauna of fish, amphibians and reptiles from beds of Clear Fork age of Texas. This chronofauna evolved with only minor influences of migration from adjacent areas. It existed on a delta that underwent modifications in topography and rainfall during the period of time studied.

Four ecological subzones inhabited by the populations of the chronofauna have been recognized from physical criteria: streams, ponds, pond margins, and flood plains and divides, called uplands. The changes of the subzones and their inhabitants through the Clear Fork show the importance of considering evolution from an ecological viewpoint. Stability of certain species and changes of others with respect to habitat and/or morphology are related to biological and physical events correlated with interrelated courses followed by populations under environmental change.

The general tendency for stability of a chronofauna under moderate environmental change stands out. As long as the various ecological niches are effectively occupied little evolution occurs. Conversely, changes that have a marked effect upon but one or a few species may initiate a chain of events that can alter the internal balance radically and result in rapid evolution. Moderately drastic changes of physical environment do not appear to have been met by adaptive modification but rather to have set in motion a series of events that led to the extinction of the chronofauna through elimination of several species essential to the maintenance of its internal balance.

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SPREAD OF THE BLACK PHASE OF THE RED-BACKED SALAMANDER IN MICHIGAN

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INTRODUCTION

For the past several years, field studies have produced information on the distribution of the red-striped and the black phases of the small terrestrial salamander, *Plethodon cinereus,* in Michigan. The two phases are similar except for the dorsum, which is black in the latter phase, while in striped individuals a broad reddish band, bounded laterally by black, extends from the head onto the tail. From evidence available, these two color phases appear to be genetically determined, having been found together repeatedly in the same brood. Information obtained to date shows their distribution in northern Michigan, which is discussed below.

The collections serving as a basis for this paper have been made mostly in selected localities by the writer, but in addition specimens in the Museum of Zoology of the University of Michigan have been examined and certain of those records included here. I am grateful to Norman E. Hartweg for the opportunity to study those specimens and to E. C. Hertzler of Kent State University, Ohio, for information on a collection he made at Burt Lake. To the Huron Mountain Club I am much indebted for permission to collect on Club property in northern Marquette County and for various kindnesses while so doing. Alfred H. Stockard kindly made available the facilities of the University of Michigan Biological Station for several short periods of collecting. My wife, Avery R. Test, was an invaluable assistant in most of the collecting. The greater part of this work was supported by grants from the Faculty Research Fund of the Horace H. Rackham School of Graduate Studies.

METHODS OF COLLECTING

The general collector usually is satisfied with a handful of specimens of any single species to establish a locality record. Such small numbers have only limited usefulness. With increasing attention being given to studies which involve moderately large samples, it is to be hoped that collectors will avail themselves of opportunities to obtain larger numbers than is customary. With accurate and precise notes on location and environment, such collections would have considerable value in many kinds of studies, particularly if specimens are collected as found rather than selected. Common sense should be exercised to keep from seriously depleting limited populations, but for at least some species our present evidence (Kline and Fuller, 1932; Test and Bingham, 1948) indicates little danger of so doing.

The area reported upon here is the Upper Peninsula of Michigan and the extreme northern tip of the Lower Peninsula, close to the Straits of Mackinac. Throughout this region the vegetation 100 years ago was largely northern hardwoods on the higher, better soil and white cedar-black spruce forest on the low ground (Gates, 1942; Potzger, 1946). The northern hardwood forest had sugar maple as the principal dominant and mixed with it were various proportions of beech, hemlock, basswood, and yellow birch. Pine forests occurred on the poorer soils. More recently, lumbering operations, fire, and clearing of the land for habitation, agriculture, and recreation have combined to modify greatly the early vegetational pattern. Few areas remain unchanged by cutting. The largest part of the land now forested is covered with either (1) north-

ern hardwoods, modified in various degrees by lumbering, or (2) birch and aspen, which have recently invaded regions swept by fire. Much of this latter type of forest is unoccupied by *Plethodon cinereus*. In general, it is the remnant of the northern hardwood forest, both modified and unmodified, in which the Red-backed Salamander now occurs and from which came the samples taken in this study. This remnant is now broken into discontinuous patches varying in size from an acre or two to several thousand acres. Not all of these contain *Plethodon*, however, for heavy grazing, frequent fires, and nearly clean timbering produce conditions in which the animal does not survive. Those woods which do contain the salamander are mostly isolated now by barriers of land unsuitable to the species. Present indications are that even in a satisfactory environment, individuals of this little animal—seldom over four inches long—do not move many yards. With their sensitivity to drying because of cutaneous respiration and terrestrial deposition of eggs, it probably does not take much cleared land to act as a barrier.

To obtain samples of sufficient size in as short a time as possible, I usually chose for collecting the most likely looking woods. These were composed of northern hardwoods with at least a few trees of some size and with dead branches and logs on the ground. Salamanders were mostly found by turning over such objects or by breaking apart the rotten logs, though an occasional individual was caught beneath the leaf litter only. Not every possible cover was investigated, but

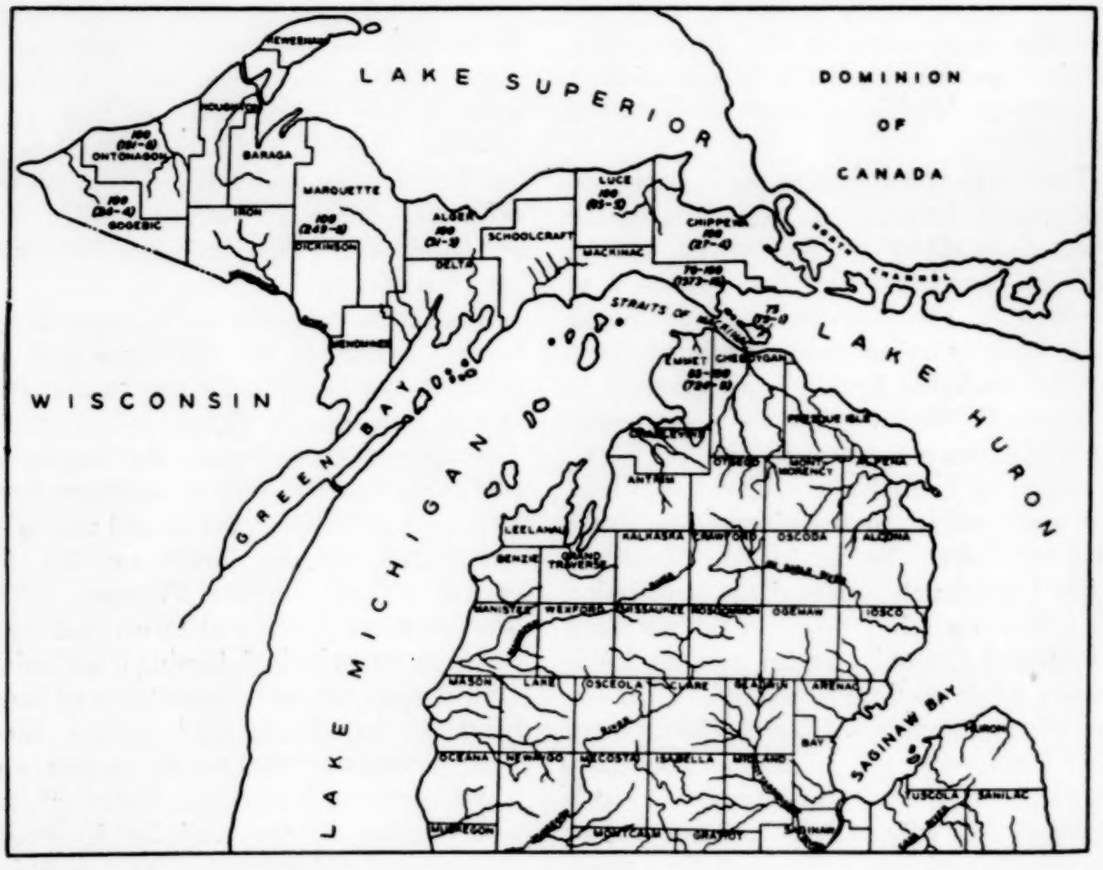

FIG. 1. Origin of samples of *Plethodon cinereus* examined from northern Michigan. The upper figures represent the percentage of the striped phase in the localities sampled within each county. (Figures for Emmet and Cheboygan counties are combined.) Of the lower pair of numbers, the first is the total individuals examined, the second the number of collecting localities represented.

TABLE 1. *Samples of* Plethodon cinereus *from populations in northern Michigan*

Location	Number of localities sampled	Size of samples	Proportion of striped individuals in per cent
Upper Peninsula			
Ontonagon Co.	8	191	100
Gogebic Co.	4	24	100
Marquette Co.	8	249	100
Alger Co.	3	31	100
Luce Co.	5	65	100
Chippewa Co.	4	27	100
Mackinac Co.			
Gros Cap	1	115	99
2.5 mi. NW Gros Cap	1	55	76
Pte. Aux Chenes	1	58	97
Other localities NW to NE of the 3 listed above	13	1,145	100
Bois Blanc Island	1	79	75
Lower Peninsula (Emmet and Cheboygan counties)			
1.5 mi. W Mackinaw City	1	59	83
1.5 mi. SW Mackinaw City	1	74	95
W end Carp Lake	1	101	94
Sturgeon Bay	1	57	91
1 mi. SW Cross Village	1	36	97
4 mi. WNW Pellston	1	98	98
Douglas Lake region	unknown	77	92
NW side Burt Lake	1	19	100
Colonial Pt., Burt Lake	1	203	95

every individual found was collected except an occasional one which escaped. Records were kept on the color of the latter. Generally, a sample was taken from an area of approximately 3–10 acres, which sometimes was the total area of the woods.

Statistically, a random sample of 100 individuals in which the less common of two types does not occur is said to indicate that this less common type comprises less than 10 per cent of the population (Simpson and Roe, 1939). In this collecting the accuracy of such a sample probably was somewhat greater, for in all woods where the black (the less common) phase occurred, black individuals were found at fairly regular intervals, indicating a rather uniform distribution in the population. It was not possible in all woods to obtain samples of 100 because of scarcity of the salamanders and lack of time, but this regularity of finding black individuals and the results of taking successive samples from the same area in a number of places elsewhere in Michigan point to the figures obtained as being reliable within 5–7 per cent (Test and Bingham, 1948; Test, unpublished data). Samples of 100 or more have somewhat greater accuracy.

Most of the collecting was done in August and September, with a small amount in early summer. That the season does not affect the proportions of the color phases collected is indicated by the results of numerous samples taken throughout the active season over the same areas in southern Michigan (Test MS.).

Samples were taken from three large populations in the Upper Peninsula, exclusive of Mackinac County where more intensive work was done. In the Porcupine Mountains State Park of Ontonagon County the population was sampled at

five places in the extensive and continuous forest, part of it virgin. Similarly, the Huron Mountains (Marquette County) collection was taken from four parts of a single large population in virgin forest. In addition, specimens from a number of other localities in the Upper Peninsula have been examined in the Museum of Zoology. Without exception, all of the 587 individuals of *Plethodon* seen from

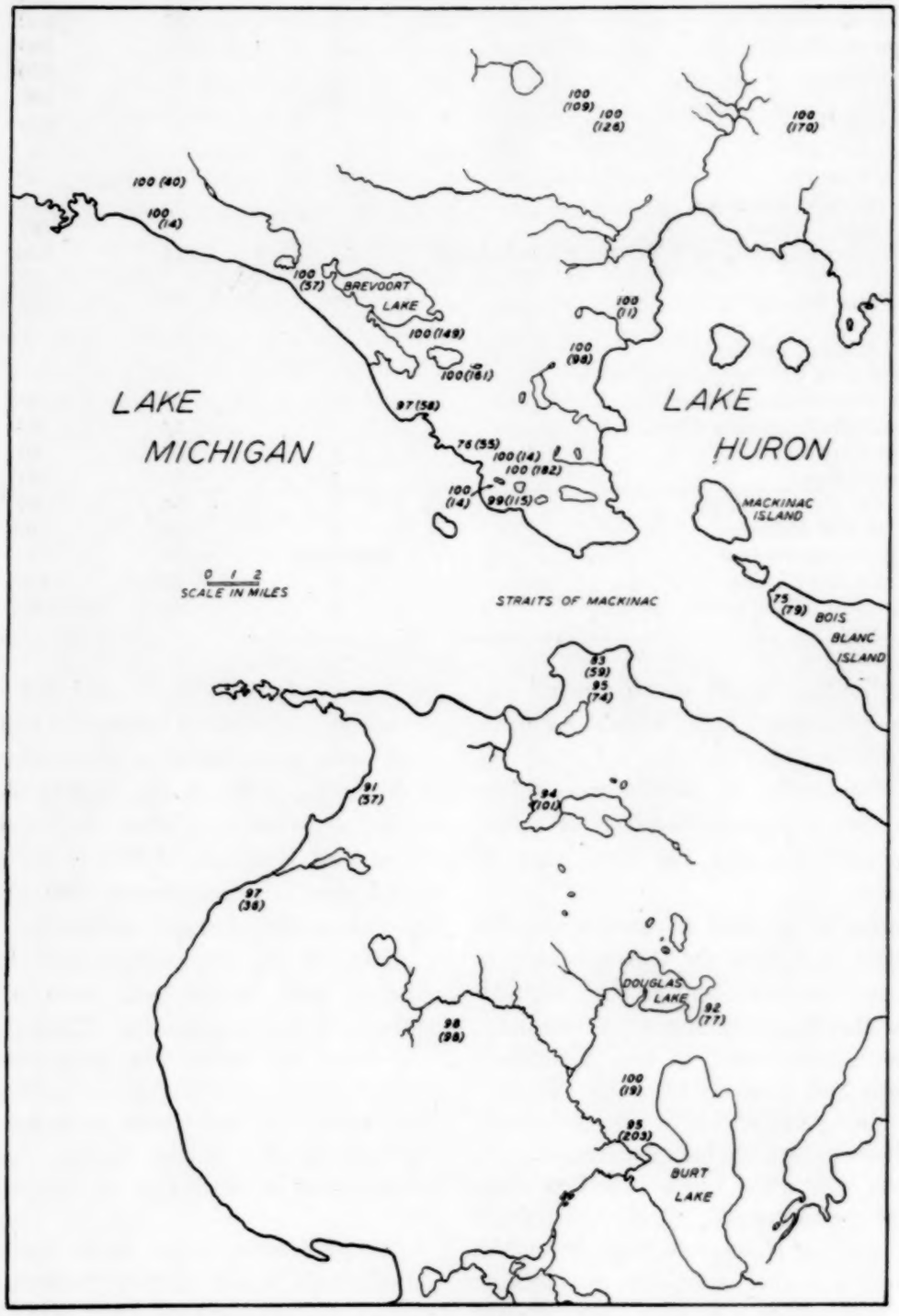

FIG. 2. Sampled populations of *Plethodon cinereus* near the Straits of Mackinac, Michigan. Positions of the figures indicate approximately the localities. The first number of each pair is the percentage of the striped phase in the sample; the number in parentheses is the total number of individuals examined.

the Upper Peninsula outside of Mackinac County have been striped. Collecting localities are shown in figure 1, and the data are listed in table 1.

After black individuals were found in Mackinac County immediately north of the straits, that region was sampled more intensively than the rest of the Upper Peninsula, collections being made at 16 places. Most of these populations are isolated from each other, but a few stations of concentration are connected by regions of low density. In figure 2 it will be seen that only three samples, all from points close to the straits and within a six-mile span, include black salamanders. The 1145 specimens in the other samples from Mackinac County are all striped.

In the vicinity of the southern shore of the straits the situation is different, for all but one of the eight samples show a small and fairly uniform proportion of black individuals. The exceptional sample is too small to be indicative. Museum specimens from the same region (but mostly without exact location data) show proportions similar to those of the majority of our samples: Of 116 from the two counties forming the northern tip of the Lower Peninsula, 91 per cent are striped. About two-thirds of those specimens are from the vicinity of Douglas Lake and are included in figure 2 and table 1.

A single collection made on Bois Blanc Island, immediately east of the straits, has 75 per cent of the specimens striped. Bois Blanc is almost completely forested, but much of the eastern part of the island apparently is uninhabited by *Plethodon* because of severe logging and perhaps fire.

Discussion

It is apparent from the data given above that the black phase of *Plethodon cinereus* is found regularly, though in low proportion, in the northern part of the Lower Peninsula of Michigan. In the Upper Peninsula, however, it is localized in a small area on the northern border of the Straits of Mackinac. To this part of the picture of distribution in Michigan may be added the knowledge that in southern Michigan the black phase usually forms a considerably larger proportion of the population (Blanchard, 1928; Test and Bingham, 1948; Test, MS.), sometimes exceeding 50 per cent.

The range of the species as a whole extends in general from Georgia north to southern Quebec and westward into Arkansas and Minnesota. Throughout this area there are few data to indicate accurately the proportions of the color phases, but it is known that both occur through most of the range. Westward and northward the black phase apparently becomes less common, and it is unknown, in the literature, west of the Mississippi River. These facts suggest that either the black phase is less well able to exist and reproduce under the environmental conditions of the north and west, or that it is evolutionarily newer than the striped phase and has not had time to spread as far. It may also be possible that each factor is in part responsible.

There have been no studies of the tolerances of the two phases, but they occur together on the Upper Peninsula near the northern limit of the species range. This suggests that different tolerances are, at least, not the sole explanation. Furthermore, environmental conditions found in the northern part of the species range are quite different from those in the western part.

Geological evidence shows that most of Michigan was covered with glacial ice as late as the Second Wisconsin (Tazewell) Substage of glaciation and the straits region as recently as the Fifth Wisconsin or Mankato (Thwaites, 1941). As the ice receded, waters of the tripartite Lake Algonquin, which overflowed the present basins of lakes Superior, Michigan, and Huron, covered the straits and the eastern half of the Upper Peninsula.

Following retreat of the ice and water, there must have been an interval before plant succession on the exposed glacial

drift reached a stage suitable for *Plethodon cinereus,* which is a forest animal. Eventually, however, it must have invaded the glaciated area from the south and slowly followed the ice northward. There is a possibility that the Upper Peninsula has become populated with the striped phase of *Plethodon cinereus* by migration from the west. If it occurred throughout its present range in earlier Pleistocene times, the driftless area of Wisconsin may have served as a refuge from which it migrated eastward into the deglaciated area. An alternative is that the salamander spread northward through Wisconsin and into the Upper Peninsula of Michigan more rapidly than across the Straits of Mackinac. There seems to be little real evidence for a choice between the three possible ways for repopulation of the Upper Peninsula by the striped phase.

If both color phases were waiting, as it were, near the southern limit of the ice sheet, it is difficult to believe that one would not have advanced approximately as rapidly as the other, producing northern populations with a large proportion of black animals. Because of the low proportion actually present, it seems more likely that the black phase invaded the glaciated region later than the striped one and that it has not yet had time to become as abundant in the north nor to spread as far.

The location and localization of the black phase on the Upper Peninsula in the immediate vicinity of the narrowest part of the Straits of Mackinac strongly indicate that it crossed there. All three colonies in which the black phase is represented are adjacent to the coast, as close as suitable conditions occur. (The tip of the peninsula at the straits is not now occupied by *Plethodon* because of the presence of the old city of St. Ignace and surrounding cleared and logged land.) Inland and farther along the coast in both directions nearly 1,150 specimens from 13 populations represent only the striped phase. It is possible that a salamander with a gene or genes for the black condition crossed the straits in a floating log, for it is well known that this species occurs frequently in logs, often laying its eggs in cavities and probably hibernating there also. It is not difficult to imagine a spring freshet washing such a log into the straits, and wind and current carrying it across. It will be noted that the black phase occurs in fair numbers within two hundred yards of the south shore of the straits even now. That only a single crossing of the black salamander occurred is suggested by the pattern of the three black phase populations on the north shore. Perhaps the landing took place near the present location of the colony containing 24 per cent blacks, at a straight line distance of about eight and a half miles from the nearest part of the Lower Peninsula, with later spread in both directions along the coast, where populations with much lower proportions of that phase now occur. It may also have spread inland a short distance from the landfall, but samples are not available from the most critical area.

Our sample from Bois Blanc Island shows that the black phase has also reached at least one of the islands in the straits and has become well established there. An attempt to find *Plethodon* on Mackinac Island was unsuccessful.

It would be useful to have a time-table in terms of years for the events postulated above. At present only estimates of uncertain validity are available, even for the geological events of the Pleistocene, although current studies of the carbon in peat may provide a much more precise dating. Recent estimates (Thwaites, 1941; Flint, 1947) of the time since the Tazewell Substage of glaciation suggest that perhaps 25,000–50,000 years have elapsed since *Plethodon cinereus* began to invade southern Michigan. Because of the salamander's small size, weak locomotor organs, and peculiarities of habit, we may assume that it spread very slowly. The region about the present Straits of Mackinac remained unavailable to terrestrial animals for a considerable interval

after retreat of glacial ice because of the high level of Lake Algonquin. The period since recession of Lake Algonquin uncovered the eastern part of the Upper Peninsula of Michigan and left the Straits of Mackinac at approximately their present width has been estimated on geological evidence (cutting of the Niagara Gorge) to be 10,000–15,000 years, and recent data from radiocarbon (Flint and Deevey, 1951) suggest that the time may have been only half as long. This period was long enough to allow the striped phase to spread throughout the region of the straits and the Upper Peninsula. In contrast, the much restricted distribution of the black phase in the Upper Peninsula suggests that it crossed the straits only a very few thousand, or perhaps hundred, years ago. Because of human modification of the forests there and consequent isolation of small remnants of the population, spread of the black phase from its present foothold, except by human agency, has ceased. Whether future commercial and agricultural developments wipe out this foothold, or whether re-establishment of suitable forest conditions allows the resumption of normal extension of range, remains to be learned.

Summary

Plethodon cinereus occurs throughout Michigan in suitable forest, forming small isolated remnants of a population that was once largely continuous. In extreme southern Michigan the black color phase forms a large proportion of the population; in the northern tip of the Lower Peninsula less than 10 per cent of the salamanders are black; on the Upper Peninsula the black phase is apparently confined to a small area at the Straits of Mackinac.

It is probable that the black phase is evolutionarily younger than the red-striped one and so has not had time to reach the limits of the species range. It probably entered Michigan long after the striped phase and only recently (perhaps 200–2,000 years ago) crossed the Straits of Mackinac. It has also reached at least one island in the straits.

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THE CONTIGUITY OF THE RANGES OF TWO SUBSPECIES OF POCKET GOPHERS

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INTRODUCTION

The present paper deals with the contiguity of the ranges of *Thomomys bottae pascalis* and *T. b. mewa* north and east of Clovis, Fresno County, California. In this part of California the pocket gopher of the Sierra foothills is *mewa* while the San Joaquin Valley is here occupied by *pascalis*. There is an exception in that *mewa* comes also out into the valley about 3 miles distant from the nearest foothills. Ingles (1950) pointed out that the zone where intergradation occurs between these races may be as much as 4 miles wide but emphasized that his data were inadequate to give an accurate estimate. He further stated that there was no visible reason why the intergrading zone should occur where it did. In order to obtain a better understanding of these and related problems it was decided to trace the zone of intergradation from Collins Corner and the Enterprise Canal, where intergrades were previously found (Ingles, 1950) to the place where the zone crossed Maple road about 10 miles to the northwest. It was also decided to try some transplants from the range of one race into that of the other.

This study was made possible by a grant, No. 1064, from the Penrose Fund through the American Philosophical Society to the senior author.

METHODS

The place of contact between the two subspecies had already been located by setting strings of McCabe traps at six different stations in north-south lines (Ingles, 1950). The purpose of this study was to investigate the sharpness of the line of contact and the possible intergradation that may have taken place there. Trapping was carried on at six stations (A–F), as located on figure 1, to the northeast of the originally discovered place of contact. This was done for two winter seasons while the animals were in full winter pelage. Only animals known to be adults on the basis of criteria given by Miller (1946) were saved and made into flat study skins. Identification of the subspecies or intergrade was made by using the linear discriminant function previously described (Ingles, 1950) using as variables the length of the hind foot (representing a measurement of a size) and red in dorsal pelage (representing a measurement of a color). All of the measurements were made by the junior author. A photoelectric reflectionmeter, Photovolt Corporation, model 610, was used for the color measurements of the pelage. The place of capture of each animal was then plotted on a map of the area (fig. 1). One hundred and sixty animals were trapped and identified. Previous study showed that all animals taken farther north and east of this intergrading zone were all *mewa* and those south and west were all *pascalis* (Ingles, 1950).

During May, 1949, 14 *pascalis* were live trapped in the San Joaquin River bottom near Fresno. These were placed in burrows on an area near Auberry from which 14 *mewa* had been removed for transplanting into the burrows of these transplanted *pascalis*. Each of the areas concerned with these inter-range transplants were slightly less than 1½ acres. They were about 20 miles apart and ranged from 250 feet (San Joaqin River bottom) to 1950 feet (Auberry Hill) in altitude.

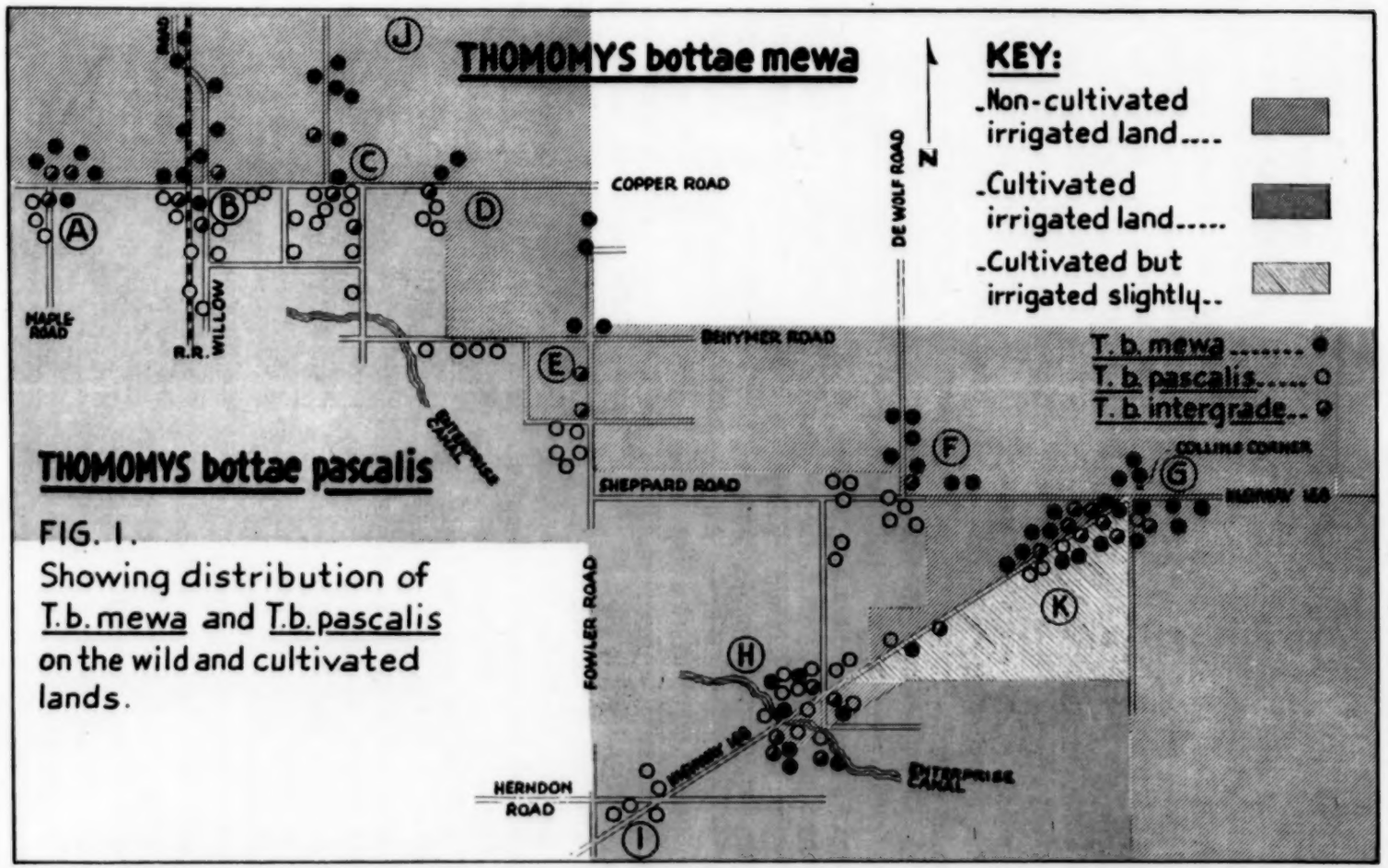

FIG. 1.
Showing distribution of T.b. mewa and T.b. pascalis on the wild and cultivated lands.

Results and Discussion

A study of the map (fig. 1) shows the contiguous distribution of the two forms with individuals intermediate in character between them. The presence of these intergrades lends evidence to the subspecific status of the two forms. The two races come in very close contact with each other between stations A through F and the intergrades occur only in a very narrow zone. This zone, in which both subspecies occur, is rarely over ½ mile wide. It is obvious that this zone of contiguity follows very closely the sharp line which separates wild uncultivated grasslands of the north and east, and the cultivated irrigated lands to the south and west. The race *mewa* inhabits the wild grasslands which become very hard and dry in summer and autumn and *pascalis* inhabits the land kept moist in the dry seasons by regular irrigations. Exceptions occur but are explainable, such as the single *mewa* that appears well down in the irrigated land at station B. This animal was actually trapped along an unmodified railroad right of way.

The distribution of the animals at stations G and H (Collin's Corner and Enterprise Canal, respectively, see Ingles, 1950) at first seem to contradict the conditions of well-defined contiguity prevailing at stations A through F. However, when it is observed that there are 3 kinds of land with respect to water and cultivation present at G and H, as well as between them, conditions at these stations become understandable. These stations and the areas between them are really ecotones and have habitats suitable for both subspecies and their intergrades. Unfortunately it was through these two stations that the survey line of the previous study (Ingles, 1950) was run and the suggestion was made that the intergrading zone might be as much as 4 miles wide. However, for 3 miles east of station G along highway No. 168, 30 gophers (not shown on map) were caught in the wild grasslands and all were identified as *mewa*. The animals caught at station I in the irrigated land were all *pascalis*.

It seems likely that the large valley race, *pascalis*, may have originally been found only in the soft, permanently moist deep soils along river bottoms, near lakes, sloughs, and springs where there is easier burrowing and more abundant vegetation. Possibly the smaller foothill race, *mewa*, originally came much farther out in the valley than it does now. Its smaller size perhaps adapts it to live in shallow drier soil with less vegetation, but it is unable to compete with *pascalis* in its original range once subsoil plowing and irrigation are introduced. An excellent chance to test this hypothesis in the near future is now in the making. Hundreds of acres of wild grassland lying southeast of station G (in the area J) are now being leveled and deep plowed (killing all of the mature *mewa*) in preparation for regular irrigations. A few *pascalis* already occupy the cultivated but rarely irrigated land at station G. The *mewa* will occupy the wild land that borders the new irrigated land on three sides. It will be interesting to see which race will eventually occupy the central area of these new fields and how the occupation will be accomplished.

All of the intergrades showed signs of sexual activity (see Miller, 1946) and in one case 3 embryos were found. The limited number of intergrades, and the narrowness of the intergrading zone (A–F) indicate that the intergrades are not so successfully adapted to the habitats as are their parents. Furthermore there is not any indication that the intergrades are more successful than either of the races in the cultivated but rarely irrigated land (a somewhat intermediate habitat). Under original valley conditions there was probably never much "intermediate area" between the moist deep soil habitat and the dry shallow soil habitat, at least in the dry seasons. The zone of intergradation has thus remained narrow because of intergrade elimination from the habitats of the parent races and because there was

no habitat, suited to the intergrades, between them where the intergrade could be dominant. Quite the opposite situation seems to exist in southern Washington where according to Dalquest and Scheffer (1944) the race *columbianus* occupies an entire county and is in itself an intergrade population between *devexus* and *aequalidens,* races of *Thomomys talpoides.*

Not one of the pocket gophers which were transplanted into the range of the other could be recovered 6 months later although 3 separate attempts were made to find them. Apparently the larger *pascalis* is no more capable of living in the shallow dry foothill soil with its less extensive plant growth which is also qualitatively different, than is the smaller *mewa* capable of living in the soft, deep, moist soil of the San Joaquin River Valley. Such negative results should not be given too much significance, however, until it is known whether transplants of *mewa,* for instance, into other parts of the *mewa* range would not also be negative.

This study seems a clear case of modification of the original environment by man to favor one subspecies at the expense of the other. The area of deep, moist soil even in dry seasons has been greatly increased and *pascalis* has taken advantage of the extension of the favorable habitat created.

The study also favors Dice's (1940) interpretation of a subspecies as being an ecological unit. It is a unit in which at least a few of the morphological and behavior characteristics, not yet known, enable it to live with a particular set of environmental factors.

Summary

The two subspecies, *Thomomys bottae pascalis* and *Thomomys bottae mewa,* come in very close contact along a ten mile zone. Some intergradation occurs along this zone, which is rarely over one-half mile wide. This zone of contiguity follows very closely the sharp line which separates the wild uncultivated grassland and the cultivated irrigated lands.

The narrowness of the zone of intergradation indicates intergrade elimination from the range of the parent races.

Transplants from the range of one race to that of the other were made with 14 *pascalis* and 15 *mewa.* The failure to recover any of these transplants after six months indicates their inability to adapt themselves to the new environment.

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PHYSIOLOGICAL PROPERTIES OF GENE ARRANGEMENT CARRIERS IN *DROSOPHILA PERSIMILIS*. I. EGG-LAYING CAPACITY AND LONGEVITY OF ADULTS [1]

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INTRODUCTION

In the Yosemite Valley area of California populations of both *Drosophila pseudoobscura* and *D. persimilis* form gradients, or clines, in relative frequencies of the gene arrangements of the third chromosome (Dobzhansky, 1948a). It has been demonstrated by competition experiments in population cages that each gene arrangement has a specific adaptive value relative to other gene arrangements and that heterozygotes of chromosomal variants from one locality may often show superior adaptive value (heterosis) with respect to the homozygotes (Dobzhansky, 1948b, Levitan, 1951, Spiess, 1950, and Wallace, 1948). In addition, the same arrangement from different localities may often have distinctly different adaptive values indicating a probable difference in gene contents.

The nature of the gradient in relative frequencies of well-established chromosomal variants along the Yosemite transect can be resolved into its component genetic and ecological parts only if definite properties can be attributed specifically to the chromosomes which take part in forming the gradient. In the search to find what properties gene arrangements may give to their carriers some success has been attained: Heuts (1948) demonstrated that different gene arrangements clearly give the flies different physiological properties, and such tests as viability of pupae and adults under various humidities and longevity of adults in relation to temperature helped explain the adaptive changes in relative frequencies of the competing types in population cages and in nature. Heterozygotes for the Standard and Chiricahua arrangements were found to be intermediate in longevity between their respective homozygotes at warm temperature but superior to homozygotes at temperatures just above freezing. Here was the first demonstration of heterosis based on physiological properties for an entire chromosome heterozygote, a fact which had been predicted on the basis of competition experiments.

Wallace has measured many physiological traits in the life cycle of "sex-ratio" and standard *D. pseudoobscura* from Piñon Flats, California. Heterozygotes for ST–SR chromosomes in females showed heterosis for nearly all traits, more strongly at warm than cool temperatures. These two arrangements of the X-chromosome differed with respect to such properties as longevity of adults, egg-laying capacity, larval competition, and sexual activity.

Dobzhansky (1950) has shown by measuring the viability of AR, CH, and ST chromosomes that the phenomenon of heterosis as observed in competition experiments between chromosomal variants from the same locality breaks down when chromosomes from different localities compete in population cages.

There are then three important facts which help to describe the functions of such chromosomal variants in the populations as a working basis for studying this altitudinal gradient: (1) At a single point in time each gene arrangement from any particular locality has its own specific adaptive value; (2) The gene combinations of each chromosomal variant are built up under the influence of natural selection within a given ecological situa-

[1] Research supported in part by a grant from the Milton Fund of Harvard University.

tion so that the same arrangement from different localities may possess different genetic properties; (3) Heterozygotes between arrangements are selected within each locality in such a way that they possess a higher "net fitness" (adaptive value) than the homozygotes. This mechanism forming heterotic combinations is necessary for the preservation of chromosomal polymorphism, since it is only when the heterozygote has a higher adaptive value than either homozygote that an equilibrium in relative frequencies of the two variants can be established (Wright, 1931).

The purpose of this series of investigations initiated herein is to discover some of the properties of third chromosome variants in *D. persimilis* taken from various localities in the Yosemite altitudinal transect, the present paper dealing with two variants from Jacksonville, California (el. 836 ft.). Traits chosen are those which would be likely to be influenced by temperature and food conditions (egg-laying capacity and longevity). The following paper in this series will be concerned with wing-beat frequency and wing area measurements which might be characteristics of the sort to be influenced by changes in air density with altitude.

Materials and Methods

All flies in these experiments were raised under constant temperature conditions (15° C.). Only flies containing the Whitney and/or Klamath gene arrangements from Jacksonville, California, were used (nine strains of Whitney and four strains of Klamath). The types of matings and culture conditions are given below. Cornmeal-molasses agar food was used, and the yeast fed to developing larvae was Fleischmann's dry brewers' yeast, type 200-B. Population cage methods have been described in previous articles (Wright and Dobzhansky, 1946); it was useful to employ these as a device for obtaining structural homozygotes without regard for the exact gene content of individual chromosomes. In such a way gene arrangements could be made homozygous while being genetically heterozygous.

The Experimental Data

The flies which were homozygous for Whitney or Klamath arrangements were obtained from population cages in the following manner: about thirty-five days after introduction of the parent flies food cups which contained pupae and were soon to produce adults were removed from the cage, and plastic tubing approximately four inches long and just the diameter of the food cups was fastened to the cups by tape and closed at the top with a cotton plug. The F_1 flies which emerged from these food cups were mated in single pairs. These data comprise experiments No. 1 and No. 2.

Individuals which were heterozygous for the two gene arrangements were obtained first by mass matings which represented all the available strains, that is, offspring of F_1 flies taken from the population cages. Fifty individuals of each sex (in separate cases using WT/WT as male or female parents) were introduced into half-pint jars. Just before the offspring from these matings were about to emerge, the parents were removed, and F_1 flies were collected on emergence. These data comprise experiments No. 3 and No. 4.

It appeared after computing the average egg-laying capacities for these flies that a repeat would be necessary for two reasons: (1) to test the significance of difference found between results of reciprocal matings and (2) to test the method of rearing. Therefore, experiments No. 5 and No. 6 were run for the initial period (see table 1) of egg-laying. Flies were reared exactly as in No. 1 and No. 2, that is from population cage food cups but with genotypes corresponding exactly to No. 3 and No. 4.

Each pair of F_1 individuals to be tested was put into a cotton-plugged 9.5×2.5 cm. vial. Vials were provided with a small plastic spoon containing a few

drops of food to which enough carbon had been added to give a black color, the smooth black surface permitting easy counting of the eggs. Just before using these spoons they were given a drop of thick yeast suspension. Spoons were changed every two or three days and the eggs on the old spoons counted. In order to keep humidity constant to prevent excessive drying of the food on the spoons as well as to permit stable conditions for the flies, the vials were stored in glass dessicators containing a saturated solution of potassium sulfate. This maintained a humidity above 90% in the dessicator. All dessicators and population cages were kept at 15° C.

Counting was done under a binocular dissection microscope, using a grid made of fine thread placed over each spoon. A record of eggs laid was kept throughout the life of the female. If the male died, another was introduced into the vial. Records of longevity are based on these females used in egg counting.

In experiments No. 1 and No. 2 consisting of homozygous Whitney and Klamath flies, respectively, one hundred females were mated, while in experiments No. 3 through No. 6 consisting of heterozygous individuals for these arrangements fifty pairs for each experiment were used (No. 3 and No. 5 represented individuals with Klamath mothers, No. 4 and No. 6 the reciprocal mating).

It was soon discovered that egg-laying was not constant from day to day, but on the contrary eggs were deposited in a roughly cyclic fashion. Egg-laying began anywhere from the sixth to twelfth day after emergence and would continue unevenly throughout the life of the fly.

TABLE 1. *Egg-laying capacity of flies WT/WT, KL/KL, and WT/KL given in average number of eggs per day for four periods arbitrarily chosen. Each average is followed by its standard error, and sample size is given below each. Probabilities of differences between means are also given, method of "t" being used*

Experiment no.	First 10 days (1–10)	Next 50 days (11–60)	Next 50 days (61–110)	Next 50 days (111–160)
1. Whitney homozygotes	15.1±0.63 n=91	15.7±0.47 n=88	13.1±0.93 n=27	5.1±0.71 n=5
2. Klamath Homozygotes	13.5±0.63 n=67	8.8±0.45 n=67	8.6±0.70 n=23	3.9±0.81 n=10
3. WT/KL from KL ♀ ♀×WT ♂ ♂	20.5±0.82 n=48	19.1±0.61 n=48	11.2±0.72 n=45	5.1±0.60 n=16
4. WT/KL from WT ♀ ♀×KL ♂ ♂	18.4±0.97 n=47	17.3±0.80 n=46	7.2±0.60 n=31	4.0±0.89 n=10
5. WT/KL from KL ♀ ♀×WT ♂ ♂	20.5±0.62 n=45			
6. WT/KL from WT ♀ ♀×KL ♂ ♂	17.6±0.59 n=38			

Probabilities: between

No. 1–No. 4=0.011	No. 1–No. 4=0.09	No. 1–No. 4<0.001	No. 1–No. 2=0.23
No. 1–No. 2=0.054	No. 1–No. 2<0.001	No. 1–No. 3=0.11	
No. 3–No. 4=0.099	No. 3–No. 4=0.09	No. 1–No. 2<0.001	
No. 1–No. 3<0.001	No. 1–No. 3<0.001	No. 2–No. 3=0.022	
No. 2–No. 3<0.001	No. 2–No. 3<0.001	No. 2–No. 4=0.14	
No. 2–No. 4<0.001	No. 2–No. 4<0.001	No. 3–No. 4<0.001	
No. 1–No. 6=0.0080	N.B. When data from No. 3 is pooled with No. 5 (pooled m=20.5±0.51) and No. 4 with No. 6 (pooled m=18.0±0.60), the probability for obtaining the difference of 2.5 by chance =0.0015.		
No. 5–No. 6=0.0014			

Every week or ten days egg production would be sustained at a level characteristic of that individual, apparently a maximum, at the end of which time few or no eggs would be deposited for an equally long period.

For this reason it was a problem to decide on the best manner of treating the data. Certainly overall production was most important. A regression line of total eggs deposited per unit time proved inappropriate because the variance along the regression increased with time. On the other hand merely an average of the total eggs laid during the individual's life would show nothing of interesting trends in maintaining or losing rates of production. It was decided finally to treat the data as follows: Only those flies which had laid eggs for ten or more days were counted. Then the total egg-laying period was divided into four parts: the first ten days followed by three fifty day periods. If an animal died during any period any eggs laid in that period were rated and recorded in the average. Such grouping of the data was used to determine whether there were any changes in pace of production and if so where the changes took place.

Table 1 gives the results for the three zygotic combinations, and several facts seem to be apparent:

1) WT/WT maintains an initial "good" production for about sixty days. It falls off slightly but not markedly until after more than one hundred days.

2) KL/KL starts with a production only a little slower than that of WT/WT (significant at the 5% level), but falls off to a level about half or a bit more than WT/WT which is maintained for about one hundred days. Eventually production falls off to a low level about equal to WT/WT at that period.

3) Heterozygotes (WT/KL) maintain a very high rate of production which is superior to both of the other zygotic types initially and for a period of sixty days (although the difference between No. 1 and No. 4 is not highly significant during the 11–60 day period). The fall-off period after sixty days is quite rapid, and production after one hundred days is equivalent to that of the homozygous types, although flies derived from WT mothers fall off more rapidly than those from KL mothers.

4) The type of rearing (either in population cage food cups or in crowded half-pint jars) does not seem to affect egg-laying since heterozygotes of the same origin have remarkably similar capacity averages for the initial period (compare No. 3 and No. 5, No. 4 and No. 6).

5) The difference which appeared not significant between reciprocal heterozygotes' egg production for No. 3 and No. 4 is repeated in experiments No. 5 and No. 6. Evidently the difference is a real one (pooled difference of 2.5 has a probability of 0.0015 that it is owing to chance alone) and is, to say the least, surprising and provocative. It should be noted that the higher egg production is found in those heterozygotes derived from the lower egg-producing mother, or in other words the chromosome derived from the male parent seems to have a dominant effect.

The maximum number of eggs produced by the three types were as follows: WT/WT produced 2,328 in 160 days of laying, KL/KL 1,610 in 134 days, and WT/KL 2,378 in 136 days.

A curve of percent females surviving over the entire period of egg-laying was derived from mortality figures on the flies whose eggs were being counted (see fig. 1). Only those flies which laid any eggs were considered on this graph.

The longest-lived of the zygotic types were as follows: WT/WT 166 days after emergence, KL/KL 165 days, and WT/KL 174 days.

From these data it is evident that the homozygous types survive equally well under our experimental conditions; however, the heterozygotes without question have a slower mortality rate. It is also of interest that the total length of life under these conditions (which are closer

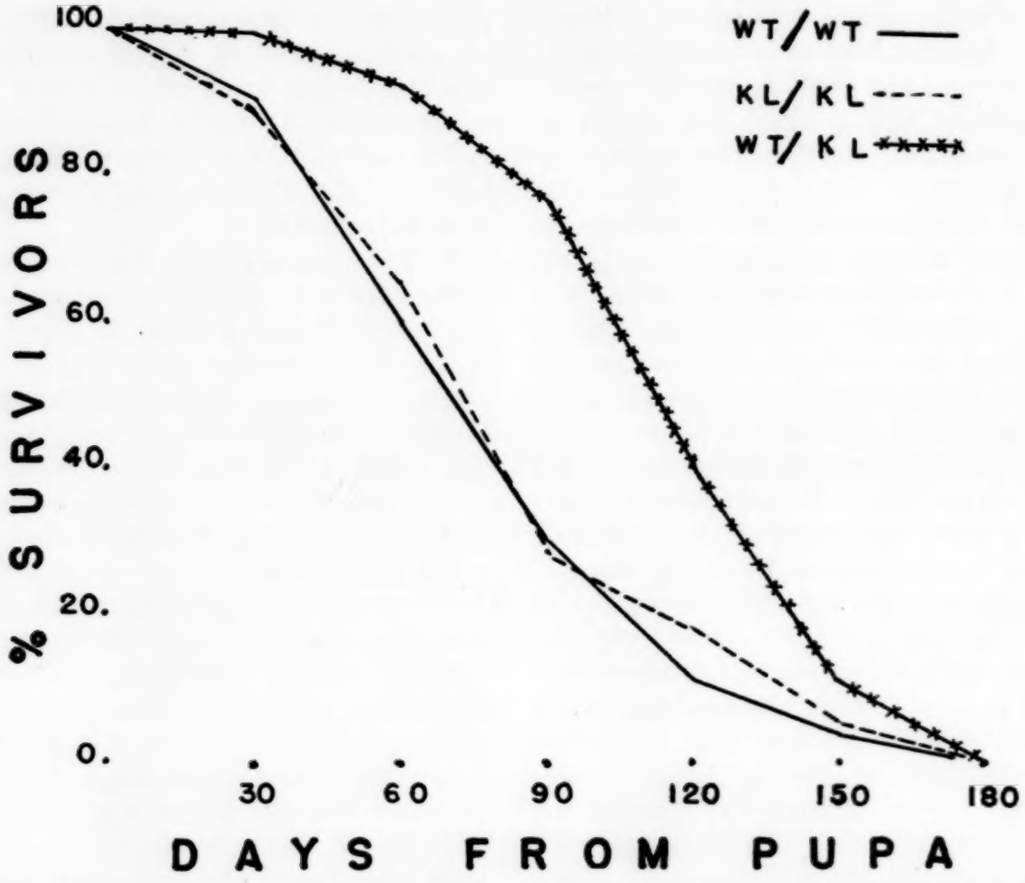

FIG. 1. Graph of survivorship for females of three zygotic types given in percent of the total number of females which laid eggs from the beginning of the experiment.

to optimal than most other laboratory conditions such as stock bottles or population cages) is more or less equivalent for all three zygotic types.

DISCUSSION

In population cage competition experiments it was shown that Whitney and Klamath arrangements of the third chromosome in *D. persimilis* from Jacksonville, California, were nearly equal in adaptive value but that an equilibrium in relative frequency was reached at about 51% WT–49% KL (Spiess, 1950). In the wild population sampled by Dobzhansky in 1947 and by Epling in 1948, WT chromosomes were most common (57% approximately) while KL and Mendocino chromosomes were next most common (KL being 23% in the February, 1948, sample). Since WT/KL must be the most common heterozygote in that locality, it would seem reasonable that natural selection would have provided that form with superior fitness as indeed the egg production and survival data appear to bear out.

When conditions are not optimal as in a population cage or under most natural conditions where competition is severe, it would be advantageous to have high initial capacity for reproduction and low mortality rate. It must be pointed out, although the concept should be clear already, that the heterozygote class is not augmented in the following generation by having these advantages; rather the essential result is that of providing for retention of the two variants in the population, that is, the polymorphic condition is thereby sustained.

It should also be noted that the heterosis exhibited by the inversion heterozygote (WT/KL) is not the result of

crossing following inbreeding. Each strain of flies is maintained by mass matings so that genetic heterogeneity is encouraged. Luxuriance due to outcrossing will have already been accounted for by crossing the strains first in a population cage and using F_1 adults as parents to provide the heterozygotes for the last two experiments. Thus this heterosis is clearly due to the heterozygosity of the third chromosome.

This phenomenon of increased egg production following hybridization has been well demonstrated in *D. melanogaster* by Gowen and Johnson (1946), who pointed out that hybrids between inbred strains start production at high levels but cannot maintain a lesser rate of loss than the inbred strains. Such is the situation with these chromosomal heterozygotes: after an initially rapid egg production the rate of loss is greater than in the homozygotes so that all types produce at the same rate in senesence.

As to the differences between the homozygotes, it is apparent from table 1 that WT/WT and KL/KL flies show dissimilar patterns: the first of these maintain essentially a rather high production for a very long period extending for about one hundred days (about 13–15 eggs per day average); KL flies on the other hand start with approximately this rate (WT and KL are barely significantly different, $p = 0.054$, for the first period) but fall off to about 8–9 eggs per day during the period of one hundred days following. It is interesting to note that in senescence both WT and KL flies produce essentially at the same rate. Certainly natural selection would have built up genetic combinations for high production in the earliest period of adult life and would have had no chance to act on the period of senescence, so that we would not expect to find adaptive differences during that period.

The equality between WT and KL for initial egg production as well as for survival tends to parallel the observation that in population cages at 16° C. equilibrium values are about the fifty per cent mark with a possibly slightly higher value for WT than for KL. Certainly these two factors must be strong contributors to the "net fitness" of the genotype; but since there are so many other factors not yet reckoned with, it would not yet be possible to attribute the competition results to any factors in a quantitative way.

Mechanisms of heterosis have been reviewed recently by Crow (1948) and Brieger (1950). By the logic of population genetics based on known mutation rates for lethal and semi-lethal recessive genes, these authors have pointed out the greater plausibility of explaining the heterotic mechanism by postulating an interallelic action as responsible rather than the dominance of increased vigor genes. Dobzhansky (1950) has suggested that in the case of chromosomal heterosis, the mechanism is one of interaction between polygene complexes which have been mutually adapted by natural selection. From the evidence presented here it would seem altogether more reasonable to assume such interallelic action the cause of the heterosis than to postulate the presence of specific dominant vigor modifiers in one chrosomal variant not found in the other since certainly mutation rates must be equal in both WT and KL, and all the increased vigor to be obtained from dominant vigor modifiers would already be manifested in the mixing of homozygous strains previous to crossing the chromosomal variants. One might argue that the dominant genes in WT would not be the same as those in KL necessarily, but when we remember the origin of the adaptation as a "mutual adjustment" in the heterozygote we see the greater reasonableness in believing that the heterozygosity *per se* of alleles might do the job perfectly well.

The significant difference observed between heterozygotes for WT/KL obtained by reciprocal matings must be accounted for. We cannot assume that

the cytoplasms of eggs laid by WT/WT females is intrinsically different from that of eggs laid by KL/KL females because these flies were mass mated in random strain crosses in order to rule out all differences in genotype except those produced by genes on the third chromosome. Therefore, it seems we are forced to the conclusion that these alternate cytoplasms are in some way conditioned by the genes of the third chromosome. Now by referring back to table 1, if we accept the statistics as showing a real difference, we must also accept this rather peculiar effect: higher egg production results from the mating in which the female was of the lower production genotype and vice versa, or to state that fact another way, the male chromosome has a dominant effect.

Let it be proposed as an hypothesis that the female parent's third chromosome has some conditioning effect on its egg cytoplasm. Further let it be assumed that the magnitude of heterosis produced by heterozygosis of third chromosome alleles would be equal irrespective of the direction of crossing. Let it be suggested, therefore, that the dominant effect of the chromosome contributed by the male is a reaction with the preconditioned egg cytoplasm in some such manner as the following: If the amount of heterosis due to heterozygosity of nuclear genes be given an arbitrary value of 4, let us assume, since the WT/WT genotype gives the greater egg production, that the WT chromosome can react heterotically with cytoplasmic products produced by the KL/KL genotype giving a heterosis value of 2 to this reaction and an accompanying net increase of 6 to the F_1 individuals. On the other hand, a KL chromosome introduced from the male parent would have less reaction with WT-conditioned cytoplasm giving only a factor of 1 or a net increase of 5.

Such a scheme as this involves two concepts not yet tested: (1) Conditioning of cytoplasm by nuclear genes, presumably by making available certain products for the reaction with the male nuclear genes or their products; and (2) A heterotic effect resulting from this reaction.

Summary

(1) *Drosophila persimilis* homozygous for the Whitney or Klamath gene arrangements of the third chromosome although heterozygous genetically differ in egg-laying capacity. WT flies maintain a moderately high rate of production (13–15 eggs per day) for about one hundred days at 15° C. under optimal conditions. KL flies begin at a rate significantly different (5% level) from that of WT (the mean is slightly lower), then soon fall off to approximately 8–9 eggs per day.

(2) Heterozygotes from either WT or KL mothers maintain a high rate of production (17–20 eggs per day) for the first sixty days, thereafter falling off rapidly to rates essentially the same as those for the homozygous flies. Those derived from WT mothers seem to fall off faster than those from KL mothers.

(3) All three zygotic combinations produce equally in senescence, a fact which might be expected since natural selection would have built up genetic combinations for high production in early life.

(4) Egg production was the same for heterozygous females whether reared in population cage food cups or in crowded half-pint jars.

(5) Both homozygous types survive equally well under these experimental conditions, but heterozygotes have a lower mortality rate. All three seem to be equally long-lived, however.

(6) The mechanism of heterosis here is more plausibly that of the interaction of heterozygotic loci than the presence of dominant increased vigor loci.

(7) Heterozygotes produced by reciprocal matings differ significantly in

egg production suggesting some cytoplasmic differences involved in the heterosis effect.

(8) A scheme for explaining this reciprocal effect is introduced, proposing a preconditioning of cytoplasm by nuclear genes, and heterosis resulting from a reaction of male nuclear genes with such conditioned cytoplasm.

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ADAPTIVE RESPONSES OF SOME THIRD CHROMOSOME TYPES OF *DROSOPHILA PSEUDOOBSCURA* [1]

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INTRODUCTION

There are several third chromosome types in natural populations of *Drosophila pseudoobscura*. These chromosome types are known to differ in gene arrangement because of a series of simple and overlapping inversions (Dobzhansky and Epling, 1944). Three arrangements are common in the fly population in the San Jacinto Mountains of southern California; namely, Standard (ST), Chiricahua (CH), and Arrowhead (AR). Two other arrangements, Treeline and Santa Cruz, are present in very low frequency. The frequencies of the ST and CH arrangements in the population there change cyclically from season to season during the year. Arrowhead, Treeline, and Santa Cruz fluctuate around the same mean throughout the year (Dobzhansky, 1947a). Standard is of low frequency in the spring, increases during the summer months and evidently maintains a relative high frequency during the fall and winter months. Chiricahua, on the other hand, reaches its maximum during June and falls in frequency during the summer. This cyclic change of frequency has persisted since 1939 (Dobzhansky, 1947a; Epling and Mitchell, in ed.). Dobzhansky has also found that the frequency of Standard/Chiricahua heterozygotes in this wild population is greater than would be expected on the basis of the Hardy-Weinberg formula.

A similar change in frequency of Standard chromosomes at the expense of Chiricahua chromosomes has been demonstrated by Wright and Dobzhansky (1946) in artificial populations grown in cages. In cages maintained at 25° C. they repeatedly observed that the frequency of ST chromosomes increased and that of the CH chromosomes decreased until an equilibrium was reached at about 70% ST and 30% CH. The population in the cage then consisted of ST/ST homozygotes, ST/CH heterozygotes, and CH/CH homozygotes. Populations maintained in cages at 15° C. showed no change of initial frequencies. The process which occurs in nature accordingly appears to be partially reproduced in the population cages at 25° C.

This experimental result led Dobzhansky to the conclusion that the carriers of Standard chromosomes are better adapted to higher temperatures than those carrying Chiricahua chromosomes and that (1947b) the most reasonable explanation of the cyclic change at Piñon Flat is the differential survival of the carriers of these arrangements in accord with the differences of seasonal environments. Since crossing over between the chromosome types is known to be greatly reduced (Dobzhansky and Epling, 1948), each type is accordingly maintained to a considerable degree as a genetic entity, thus permitting differences in the adaptive character of each.

There is little evidence for the causes of adaptive differences between the chromosome types. The investigation reported here is an attempt to determine the nature and extent of adaptive differences, if any, between the ST/ST, ST/

[1] This work was done at the University of California at Los Angeles and was submitted to the Graduate Division in partial fulfillment of the requirements for the degree of Doctor of Philosophy.

[2] This work was completed while the author was a National Research Council Predoctoral Fellow of the Atomic Energy Commission in the Biological Sciences.

CH, and CH/CH chromosome types from Piñon Flat.

The Egg and Larval Stages

Dobzhansky (1947b) has shown that when a sample of eggs is removed from a population cage, maintained at 25° C. and the larvae hatched from them are grown without crowding and with a good supply of food there is, upon examination of the salivary gland chromosomes, no significant departure from the Hardy-Weinberg formula. Consequently Dobzhansky concluded that the replacement of one chromosome type by another which is noted in the population cages and in nature is due to differential mortality at some time after the eggs are laid. However, both in nature and in the population cage, the eggs of one type might be killed more often than those of another by different temperatures. Or, being equally viable at different temperatures, one type might tend to develop and hatch more rapidly at certain temperatures. If the latter were true, the first larvae to hatch would not only reach the food source sooner but would also modify it for the late comers, as Chiang and Hodson (1950) and Sang (1950) have shown. Under artificial conditions, such as those they described, the first larvae to hatch disturb the food and bury and crush the unhatched eggs and thus decrease their viability.

The conditions to which larvae of *D. pseudoobscura* are subjected to in nature at Piñon Flat can only be inferred from what is known of their feeding sites in slime fluxes at Mather, California (Carson, 1951) and occasional observations elsewhere, for the feeding sites at Piñon Flat are unknown. Slime fluxes are moist or even semi-liquid, hence the atmospheric humidity presumably has little or no direct influence on the larvae. The artificial medium in the population cage is also moist. Temperature has a direct effect, however, and da Cunha (1951) has also shown differences of effect of different yeasts on populations of *D. pseudoobscura* maintained in cages. A reasonable conjecture would be that larvae of different chromosome types of *D. pseudoobscura* might react differently to temperature or to wild yeasts or to both.

Material

Ten stocks of ST/ST and ten of CH/CH were used in all of the experiments reported in this paper. These stocks were obtained from wild females captured in 1950 at Piñon Flat. The progeny of each female was pair mated until a structurally homozygous stock was found on examination of the salivary gland chromosomes (the determinations were made by Professor Carl Epling and Mr. Donald F. Mitchell at the University of California at Los Angeles). In order to restore genetic heterozygosity the experimental ST/ST homozygotes were obtained by intercrossing the ten stocks of the ST/ST homozygotes from the wild collection. The experimental CH/CH homozygotes were obtained in a similar fashion by intercrossing the ten CH/CH wild stocks. The experimental ST/CH heterozygotes were obtained by intercrossing flies from the ten ST/ST wild

Table 1. *Total egg hatch in per cent*

	25° C.			15° C.		
Chromosome type	ST/ST	ST/CH	CH/CH	ST/ST	ST/CH	CH/CH
Total eggs	458	558	745	262	345	281
Total hatch	449	521	698	259	338	281
Per cent hatch	98.03	93.36	93.69	98.85	97.97	100
Per cent trans. to $\sin^2\theta$*	82.51	75.11	75.46	83.71	81.67	90.0

* The per cent values have been transformed to $\sin^2\theta$ in order to compensate for initial differences in total egg numbers in each experiment.

collections with the ten CH/CH wild collections.

Because of the uniformity in adaptive responses of all of the chromosome types in the experiments discussed below, the data have been presented in summary only.

Egg Stage

Details of the methods for the collecting and handling of eggs and larvae will not be presented here (see Sonnenblick, 1950 and Spencer, 1950). The results of experiments testing the effects of temperature upon egg viability are summarized in table 1. This table shows the total per cent of eggs hatched in three replications of the experiment at 25° C. and the total per cent in two replications at 15° C., that is egg viability at 25° and 15° C. P values from the *t* test are not significant ($P > 0.05$). No eggs hatched at 30° C. which temperature is accordingly lethal. Table 2 and figures 1 and 2 show the egg hatching rates at 15° C. and 25° C. for three replications. It appears that there are no differences between the chromosome types. The rate at the lower temperature is, as might be expected, slower. In order to ascertain if there were any differences of the rate of egg hatching between the chromosome types a comparison was made of the slopes of the curves for the 24–32 hour period at 25° C. and for the 48–56 hour period at 15° C. P values from the *t* test were found to be greater than 0.05. Therefore, the differences in hatching rate between chromosome types at 15° and 25° C. are not significant.

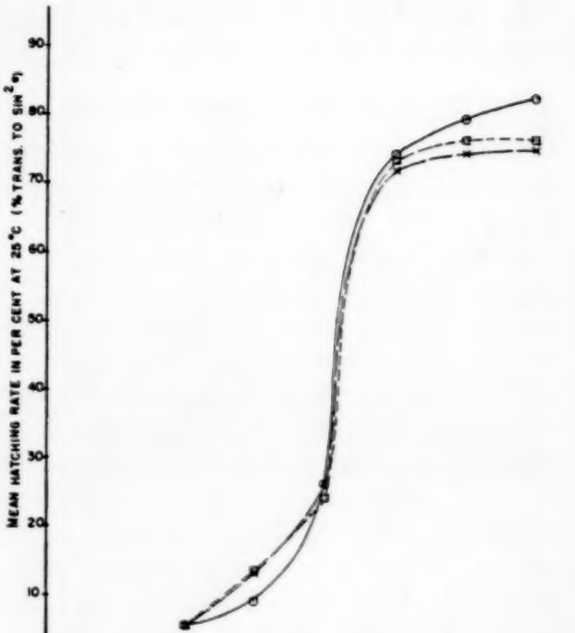

FIG. 1. Egg hatching rate at 25° C. for ST/ST (——O——), ST/CH (——X——), and CH/CH (——□——).

TABLE 2. *Mean egg hatching rate in per cent*

		25° C.			15° C.		
Chromosome type		ST/ST	ST/CH	CH/CH	ST/ST	ST/CH	CH/CH
Hours after laying	0	—	—	—	—	—	—
	8	1.08	1.04	0.996	1.14	0.855	0.315
	16	2.64	5.00	5.45	1.90	1.39	1.68
	24	19.63	19.30	16.76	3.82	3.18	2.80
	32	92.70	90.00	91.54	6.10	4.89	4.56
	40	96.20	92.63	94.13	6.86	7.40	8.50
	48	98.06	92.63	94.53	21.00	20.45	22.20
	56–104	98.06	92.63	94.53			
	56				64.80	60.50	67.85
	64				92.15	92.70	94.50
	72				99.05	96.80	98.65
	80				99.05	98.05	100.00
	88				99.05	98.05	100.00
	96				99.05	98.05	100.00
	104–152				99.05	98.05	100.00

TABLE 3. *Crowding and larval viability*

No. larvae seeded/expt.	Total no.	Total no. of pupae formed			Per cent larval survival			Per cent larval mortality		
		ST/ST	ST/CH	CH/CH	ST/ST	ST/CH	CH/CH	ST/ST	ST/CH	CH/CH
10	30	26	27	26	87	90	87	13	10	13
25	75	65	63	64	87	84	86	13	16	14
50	150	124	126	128	83	84	85	17	16	15
100	300	141	142	140	47.4	48.0	46.7	52.6	52.0	53.3

Larval Stage

The mean viability of the larvae of the three chromosome types when fed on dried brewers' yeast was found to be 88.6% for ST/ST, 88.3% for ST/CH, and 89.6% for CH/CH at 25° C. At 15° C. the mean viability was 89.6% for ST/ST, 89.6% for ST/CH, and 91.0% for CH/CH. At 30° C. the mean viability was 14% for ST/ST, 14.3% for ST/CH, and 13.3% for CH/CH. 30° C. is, therefore, a sub-lethal temperature for the larvae. P values from the *t* test were found not to be significant ($P > 0.05$ in all cases). Also larval growth rates were found to be the same for each type. They were determined by the duration of the larval stage fed on *Saccharomyces cerevisiae* and several wild yeasts which had been isolated from the crops of Piñon Flat adults.

The mean larval life for all of the three chromosome types when grown on *S. cerevisiae* was found to be 136 hours. This is true of wild strain 48–1 which is also *S. cerevisiae* and may have been ingested at some human habitation nearby the collecting ground at Piñon Flat. The duration of larval life on all of the remaining yeasts tested (48–2, –4; 49–22; 50–85, –88, –151, –174) was about 144 hours for all of the chromosome types. One other yeast, 48–3, however, delayed the larval stage to 204 hours. Again no differences were found between the three chromosome types.

The inhibition of pupation of the larvae of *D. pseudoobscura* grown on yeast 48–3 may be caused by deficiencies of certain substances required by them for the normal course of development. Thus, when larvae kept for 150 hours on yeast 48–3 were removed and placed on bakers' yeast, their subsequent development was normal. This yeast may not therefore be the customary food of the larvae at Piñon Flat, even though isolated from adults found there. Carson (1951) has found at Mather that the adults do not always feed where the larvae feed. When more is known of the larval feeding sites at Piñon Flat, a further study of the effects of the wild yeasts on larval development may yield other information.

Another factor which might have an effect on the differential survival of the chromosome types is that of competition for food during the larval stage. In the population cage the three chromosome types are in continual competition for

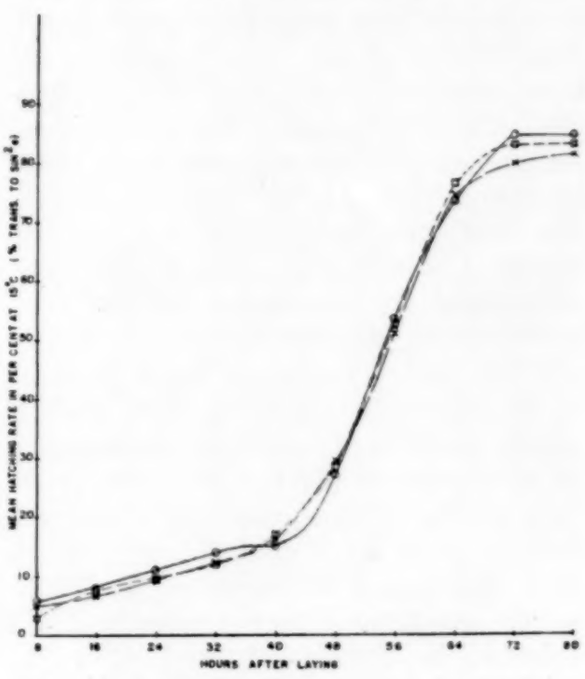

FIG. 2. Egg hatching rate at 15° C. for ST/ST (——O——), ST/CH (——X——), and CH/CH (---□---).

food during both the larval and adult stages. If larvae of one chromosome type can compete more successfully under crowded conditions than another then this type would have a better chance for survival. To test this possibility 10, 25, 50, and 100 larvae of each chromosome type were placed in vials containing living bakers' yeast and 2% dried yeast. The cultures were kept at 25° C. The summation of the results of three experiments is shown in table 3. It can be seen that larval mortality increases sharply with 100 larvae per culture, but that there are no significant differences between the three different chromosome types.

The Pupal Stage

Ellwyn (1917) and Geisler (1947) have shown that the relative humidity of the atmosphere affects the viability of pupae of *D. melanogaster*. The lower the relative humidity the greater is the pupal mortality. Heuts (1947 and 1948) has recently investigated the effect of relative humidity on the viability on Piñon ST/ST and CH/CH purpae. Reasoning from the fact that ST chromosomes increase in frequency at Piñon Fat during the drier part of the year he concluded that ST/ST pupae would probably be more viable at lower relative humidities than CH/CH pupae. To test this he set up two population cages, using them simply as sources for abundant pupae. The first contained ST/ST flies and the second CH/CH flies. Each cage was established by combining 10 different stocks of ST/ST and 10 different stocks of CH/CH. When pupae began to form in the cages he removed them with a needle and placed one hundred pupae in each of several glass vials. The vials were covered with cheese cloth which was held in place by a rubber band. They were then placed in desiccators at 25° C. which contained different saturated salt solutions in order to obtain relative humidities of 100%, 92%, 76%, 56%, and 0%. According to Heuts, CH/CH pupae are more viable than ST/ST at 100% relative humidity while the reverse is true at 92% relative humidity. These results are to be questioned for two reasons. First, since he presents no statistical analysis of the data the probable significance of the differences in pupal viability which he lists cannot be ascertained. Secondly, it is doubtful whether the difference of 8% between 100% and 92% relative humidity which Heuts reported was actually maintained in his chambers. The relative humidity of air over water may vary and the same is true of the salt solutions he used and for those used here.

Because Heuts' results were the first, and thus far the only indication of differences in adaptive response between ST/ST and CH/CH chromosome types, it seemed advisable to repeat his experiment and to extend the investigation to other temperatures.

Methods

Pupae for the experiments were derived from crosses mentioned above. Larvae were allowed to pupate in culture bottles at 25° C. The medium was prepared with dried yeast and in addition the larvae were kept well supplied with growing bakers' yeast to insure normal larval development. Sang (1950) has shown that a reduced food supply during the larval stage can affect pupal and adult viability. Pupae one hour old or less were picked from the bottles with a fine needle and placed on the inner wall of glass vials, usually one hundred pupae per vial. At this age the pupae adhere readily to the glass. The vials were then covered with gauze held in place by rubber bands and set in a temperature-humidity control chamber.

Desiccators were used for the humidity chambers. They were placed in incubators at 15°, 25°, and 30° C. Different relative humidities were obtained by the use of saturated solutions of various salts following O'Brien (1948). Similar solutions were used by Heuts in his experiments.

In the experiments reported here the

relative humidities used are indicated in column one of table 4.

Results

In general the relative humidity of the atmosphere was found to have a definite effect on pupal viability. Failure of metamorphosis was observed to some extent at all humidities. Death at relative humidities above 76% were few, however, and may have been caused in part by handling. At 0% relative humidity failure of metamorphosis was complete. Emergence was generally normal at 76% and higher, but was usually incomplete at 56%, even though metamorphosis appeared to be normal. Many flies would emerge only partly and die. The data are presented in table 4 and figure 3. An analysis of variance shows that different humidities have significantly different effects on metamorphosis and eclosion and that the reaction of different chromosome types is significantly different at 76% and 56%. Contrary to Heuts' report, there are no significant differences at 92% and 100%. Similar experiments were made at 15° C. (100% and 0% relative humidity) and at 30° C. (100%, 92%, 75%, 51%, 33%, and 0% relative humidity). Metamorphosis and eclosion were as normal at 15° C. and 100% relative humidity as at 25° C. and 100% relative humidity. All died at 0% relative humidity. Very few adults developed normally and emerged at 30° C. This temperature is accordingly lethal or sublethal. Those which emerged did so only at 92.5% and 100% relative humidity. The remainder died. No differences between chromosome types were found at these temperatures.

TABLE 4. *Humidity and pupal viability at 25° C.*

Exper. no. . . .		1			2			3			Total pupae	Total adults	Per-cent
Rel. hum.	Chr. type	No. of pupae	No. of adults	Per cent	No. of pupae	No. of adults	Per cent	No. of pupae	No. of adults	Per cent			
100	ST/ST	200	188	94.0	200	193	96.5	200	190	95.0	600	571	95.2
100	ST/CH	200	191	95.5	200	190	95.0	200	193	96.5	600	574	95.6
100	CH/CH	200	197	93.5	200	191	95.0	200	194	97.0	600	582	95.1
92	ST/ST	200	196	98.0	200	195	97.5	200	195	97.5	600	586	97.6
92	ST/CH	200	194	97.0	200	194	97.0	200	196	98.0	600	584	97.3
92	CH/CH	200	194	97.0	200	196	98.0	200	193	96.5	600	583	97.2
76	ST/ST	200	192	96.0	200	194	97.0	200	196	98.0	600	582	97.0
76	ST/CH	200	163	81.5	200	169	84.5	200	167	83.5	600	499	83.2
76	CH/CH	200	176	88.0	200	173	86.5	200	172	86.0	600	521	86.8
56	ST/ST	200	94	47.0	200	102	51.0	200	99	49.5	600	295	49.2
56	ST/CH	200	72	36.0	200	74	37.0	200	76	38.0	600	222	37.0
56	CH/CH	200	44	22.0	200	41	20.5	200	40	20.0	600	125	20.8
43	ST/ST	—	—	—	—	—	—	200	92	46.5	200	92	46.5
43	ST/CH	—	—	—	—	—	—	200	73	36.5	200	73	36.5
43	CH/CH	—	—	—	—	—	—	200	36	18.0	200	36	18.0
33	ST/ST	—	—	—	—	—	—	200	86	43.0	200	86	43.0
33	ST/CH	—	—	—	—	—	—	200	69	34.5	200	69	34.5
33	CH/CH	—	—	—	—	—	—	200	32	16.0	200	32	16.0
19	ST/ST	—	—	—	—	—	—	200	24	12.0	200	24	12.0
19	ST/CH	—	—	—	—	—	—	200	13	6.5	200	13	6.5
19	CH/CH	—	—	—	—	—	—	200	10	5.0	200	10	5.0
13	ST/ST	—	—	—	—	—	—	200	0	0	200	0	0
13	ST/CH	—	—	—	—	—	—	200	0	0	200	0	0
13	CH/CH	—	—	—	—	—	—	200	0	0	200	0	0
0	ST/ST	200	0	0	200	0	0	200	0	0	600	0	0
0	ST/CH	200	0	0	200	0	0	200	0	0	600	0	0
0	CH/CH	200	0	0	200	0	0	200	0	0	600	0	0

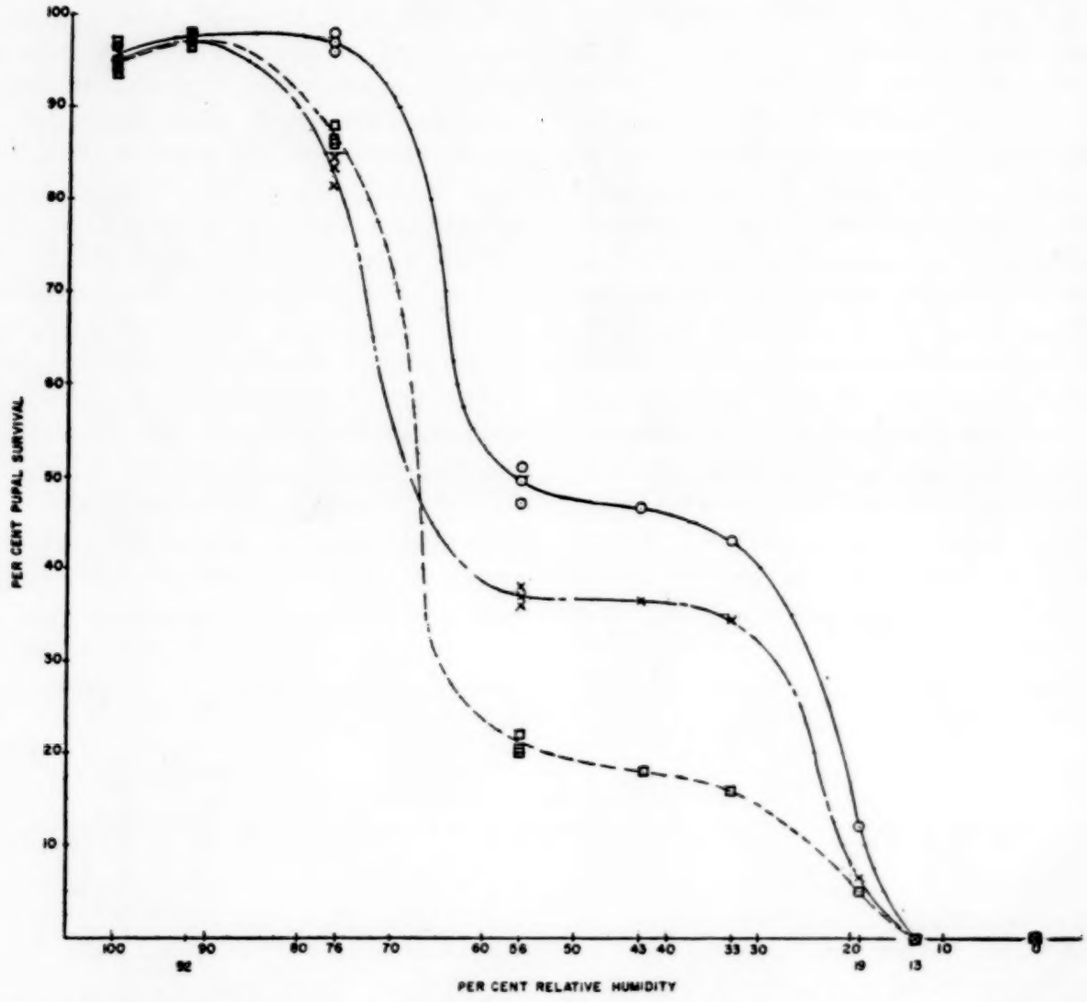

FIG. 3. Viability of ST/ST, ST/CH, and CH/CH pupae at 100%, 92%, 76%, 56%, 43%, 33%, 19%, 13%, and 0% relative humidities at 25° C. Symbols are the same as in figure 1.

The only humidities at which Heuts compared the relative viability of Standard and Chiricahua types were 100%, 92%, and 0% relative humidity. He found that more Chiricahua adults emerged at 100%, and more Standard adults at both 92% and 0% relative humidity. He obtained 6% survival at the last named. Heuts' results and those presented here are not in agreement. No differences between chromosome types were observed at 100% and 92% and no pupae survived at 0% relative humidity, at temperatures not only of 25° C. but also of 15° C. and 30° C. Survival at the humidities below 56% are consistent with those at 0% relative humidity. Nevertheless, the results presented here corroborate Heuts' conclusion that Standard pupae are less affected than Chiricahua by lower humidities and are consistent with the observed increase in Standard chromosomes at Piñon Flat as the relative humidity of the atmosphere decreases in summer. This differential response may accordingly contribute to the changes of frequency observed there.

The large survival at 0% relative humidity reported by Heuts may have been a consequence of selection of the pupae. Pupating larvae are white and glistening as they begin metamorphosis and become dull as the pupal case forms. After a certain period the anterior spiracles stop their movement. About an hour elapses until the pupae begin to turn brown and the case begins to harden. Such pupae are more likely to withstand desiccation

as Ellwyn (1917) observed. Heuts says that "only very young and light pupae were taken." Some may have begun to harden. In the present experiments the pupae used were not more than an hour old. These differences in handling may explain the different results.

There is no doubt that ST/ST and ST/CH pupae can survive lower relative humidities than CH/CH pupae, at least if they are subjected to desiccation in their earliest stages. What bearing this may have on survival in nature is obscure because so little is known of the actual conditions of pupation. Table 4 indicates that the greatest differences in survival between Standard and Chiricahua lie generally between relative humidities of 30%–60%, and it is true that this range is approximated at Piñon Flat in respect of maxima, in June and July, when Standard is beginning to increase. Nevertheless, the instances recorded by Dobzhansky and Epling (1944) when abundant pupae were found in slime fluxes on deodar, suggest that pupation and metamorphosis occur on the margins of the flux in material of the consistency of library paste. Having pupated thus under favorable conditions, the pupae may become hardened and able to withstand low humidities which would be fatal at an earlier stage. They may thus wait for humidities favorable for emergence. This is suggested by the report of abundant collecting at Piñon Flat in July (Dobzhansky and Epling, 1944) after a summer shower. The population is at its lowest density here in July and August.

The Adult Stage

The atmospheric conditions to which adult flies are subjected and in which they are active are somewhat better known than those of the pupae. They seldom come to feeding cups when the temperature is less than 10° C., regardless of the relative humidity, and at the same time are known to appear there under a wide range of relative humidities. One factor controlling such activity is light intensity (Mitchell and Epling, 1951). There is no practical way, however, of determining the chromosomal constituents of the flies which appear under different conditions in nature. Nor, because of the light relation, would there be any assurance that more adults of one type would appear at the cups than of another under the various conditions observed. The effects of temperature and relative humidity can be studied, however, by subjecting adults raised under similar conditions to various combinations of temperature and humidity. The following experiments were accordingly carried out with the object in view of learning, first, under what conditions total survival is greatest, and, second, under what conditions differences of survival may occur between different chromosome types.

Method

Adults of both sexes were obtained from the crosses described above. Twenty-four hours after emergence from culture bottles, where they were raised under optimal conditions of food and crowding, they were transferred to fresh bottles and allowed to remain in them for 24 hours. One hundred were then selected and placed in empty glass vials. Use of wet, living yeast would modify relative humidity, hence, flies must be put into empty vials. Adults, ten per vial, were set in the humidity chambers previously described. Relative humidities of 100%, 76%, 56%, 33%, 13%, and 0% were obtained at 25° C. and 100%, 75%, 51%, 31%, and 0% at 30° C. The number of survivors was counted at 12 hour intervals until all of the flies were dead.

Results

The results are presented in tables 5 and 6 and in figures 4–14. They show clearly that adults carrying the three chromosome types have different death rates at both 25° C. and 30° C.

The mean death rates of ST/ST and ST/CH adults are approximately the

TABLE 5. *Adult survival at different relative humidities at 25° C.*

Time in hours	Chromosome type and experiment no.									Mean viability		
	ST/ST			ST/CH			CH/CH					
	1	2	3	1	2	3	1	2	3	ST/ST	ST/CH	CH/CH
100% R. H.												
0	100	100	100	100	100	100	100	100	100	100	100	100
12	100	98	97	100	100	98	100	100	100	98.3	99.3	100
24	100	98	97	96	99	94	84	87	80	98.3	96.3	83.6
36	93	92	90	81	82	88	26	20	23	91.6	83.6	23.0
48	0	3	2	0	0	0	0	0	0	1.67	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0
75% R. H.												
0	100	100	100	100	100	100	100	100	100	100	100	100
12	99	100	98	100	100	100	98	96	100	99.0	100	98.0
24	94	95	92	85	80	78	73	78	76	93.6	81.0	75.6
36	54	56	50	33	39	36	10	6	3	53.3	36.0	6.3
48	0	0	0	0	0	0	0	0	0	0	0	0
60	0	0	0	0	0	0	0	0	0	0	0	0
56% R. H.												
0	100	100	100	100	100	100	100	100	100	100	100	100
12	100	97	100	98	99	97	87	85	84	99.0	98.0	85.3
24	92	90	88	75	78	77	68	62	65	90.0	76.6	65.0
36	51	48	48	14	19	11	2	1	0	49.0	14.6	1.0
48	0	0	0	0	0	0	0	0	0	0	0	0
33% R. H.												
0	100	100	100	100	100	100	100	100	100	100	100	100
12	100	100	99	96	95	93	85	81	83	99.6	94.6	83.0
24	89	85	81	71	73	69	61	58	52	85.0	71.0	57.0
36	48	45	41	9	10	8	0	0	0	44.6	9.0	0
48	0	0	0	0	0	0	0	0	0	0	0	0
13% R. H.												
0	100	100	100	100	100	100	100	100	100	100	100	100
12	94	99	91	90	91	89	76	79	81	94.6	90.0	78.6
24	70	69	73	46	42	40	0	0	0	70.6	42.6	0
36	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0
0% R. H.												
0	100	100	100	100	100	100	100	100	100	100	100	100
12	93	96	90	92	89	90	80	77	79	93.0	90.3	78.6
24	68	65	61	42	45	44	0	0	0	64.6	43.6	0
36	0	0	0	0	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0	0	0	0	0

TABLE 6. *Adult survival at different relative humidities at 30° C.*

Time in hours	Chromosome type and experiment no.									Mean viability		
	ST/ST			ST/CH			CH/CH					
	1	2	3	1	2	3	1	2	3	ST/ST	ST/CH	CH/CH
						100% R. H.						
0	100	100	100	100	100	100	100	100	100	100	100	100
12	98	100	99	99	98	100	100	100	96	99	98	98.6
24	89	86	88	82	80	83	41	40	46	87.6	81.6	42.3
36	56	55	53	48	48	45	0	0	0	54.6	47.0	0
48	0	0	0	0	0	0	0	0	0	0	0	0
						75% R. H.						
0	100	100	100	100	100	100	100	100	100	100	100	100
12	100	99	100	100	100	97	82	84	80	99.6	99	82.0
24	73	71	69	69	64	63	25	22	21	71	65.3	22.6
36	21	25	28	20	24	27	0	0	0	24.6	23.6	0
48	0	0	0	0	0	0	0	0	0	0	0	0
						51% R. H.						
0	100	100	100	100	100	100	100	100	100	100	100	100
12	93	95	97	94	92	95	75	76	78	95.0	93.6	76.3
24	66	67	60	61	63	60	5	9	4	64.3	61.3	6.0
36	18	10	19	6	8	5	0	0	0	15.6	6.3	0
48	0	0	0	0	0	0	0	0	0	0	0	0
						31% R. H.						
0	100	100	100	100	100	100	100	100	100	100	100	100
12	91	90	89	89	88	91	62	61	64	90	89.3	62.3
24	50	53	52	47	43	46	4	3	2	51.6	45.3	3
36	5	6	3	3	5	6	0	0	0	4.6	4.6	0
48	0	0	0	0	0	0	0	0	0	0	0	0
						0% R. H.						
0	100	100	100	100	100	100	100	100	100	100	100	100
12	80	84	88	65	62	60	0	0	0	84	62.3	0
24	0	0	0	0	0	0	0	0	0	0	0	0

same at 25° C. and 100% relative humidity, however, that of CH/CH is significantly higher. At 36 hours after the start of the experiment only 23% of the CH/CH adults were alive and there remained about 91.6% ST/ST and 83% ST/CH adults. Thus, death rate of CH/CH adults begins to increase until 36 hours. After 48 hours the flies of all three chromosome types are dead. CH/CH adults appear to be less adapted to 25° C. and 100% relative humidity than are ST/ST and ST/CH adults. At the other humidities at 25° C. there is a similar pattern of survival except for the fact that the heterozygote is in intermediate survival between ST/ST and CH/CH. Study of figures 4–14 will

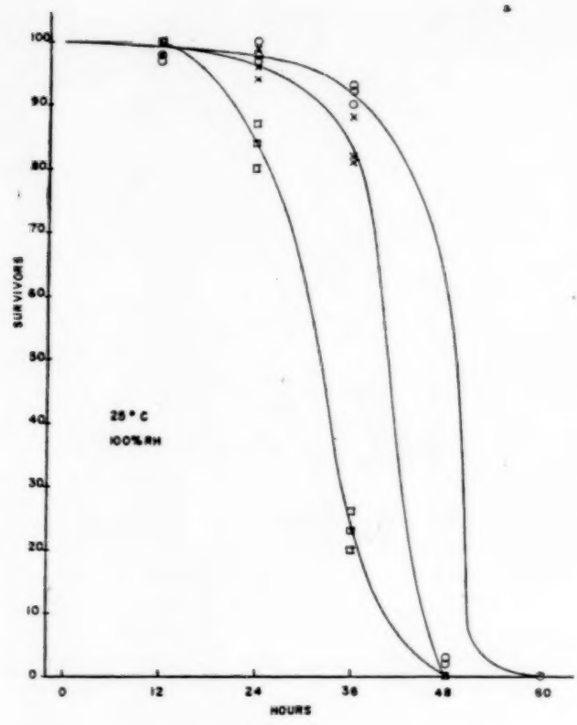

FIG. 4.

FIGS. 4–14. Adult survival at different relative humidities at 25° and 30° C. ST/ST (——O——), ST/CH (——X——), and CH/CH (——□——).

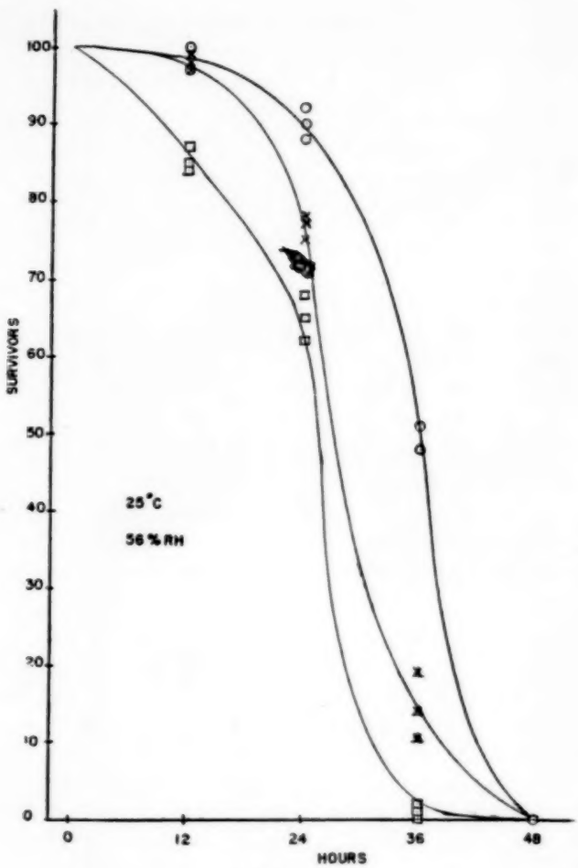

FIG. 6.

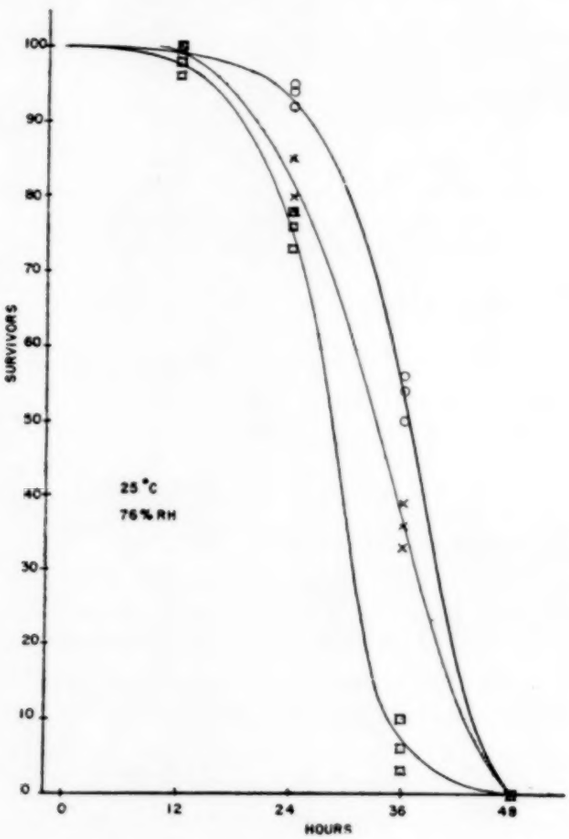

FIG. 5.

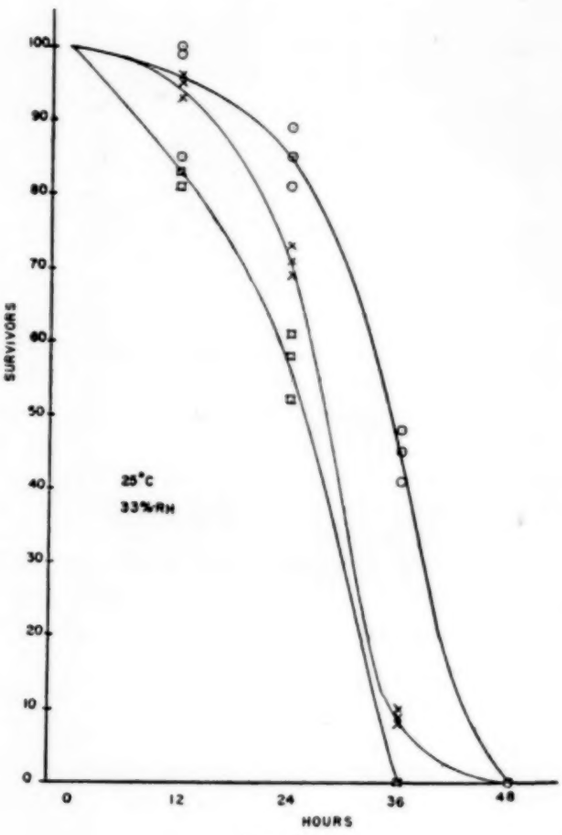

FIG. 7.

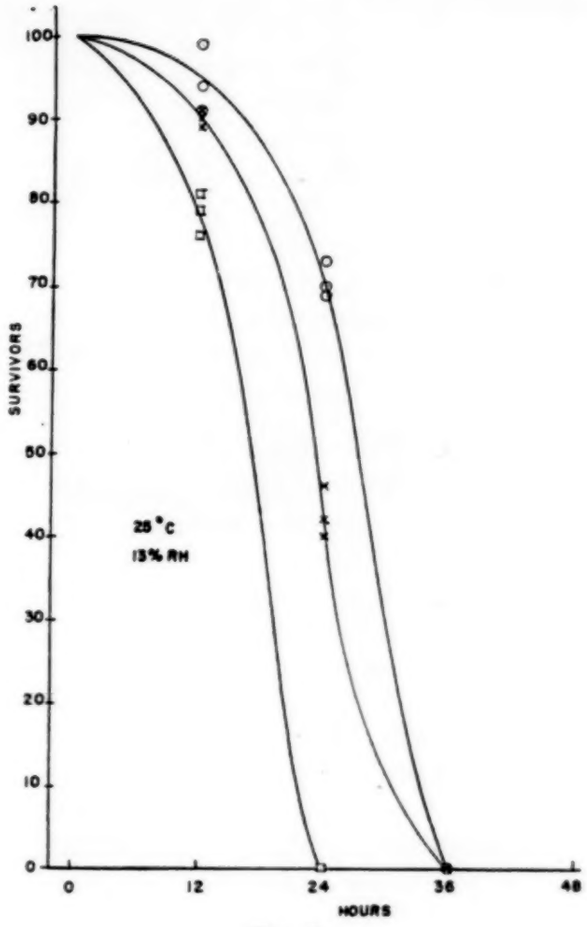

FIG. 8.

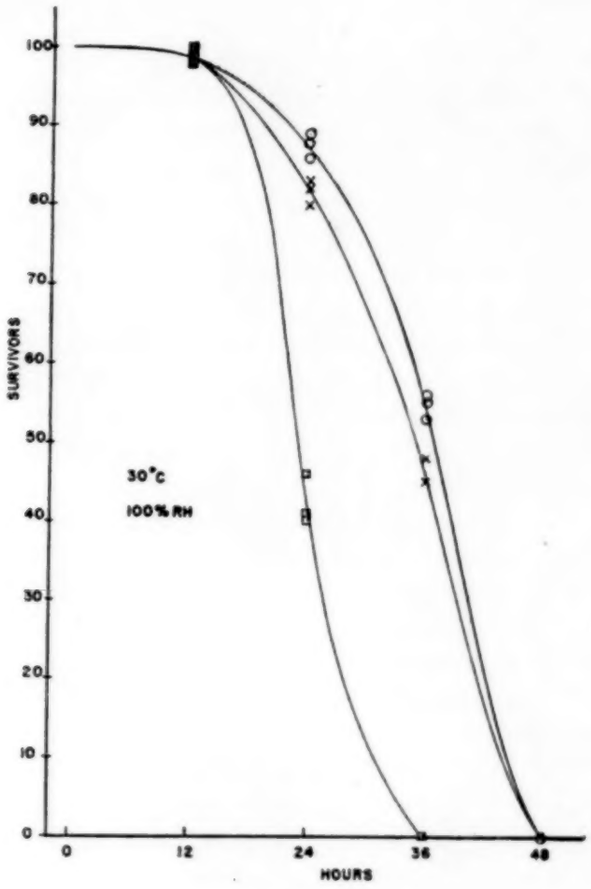

FIG. 10.

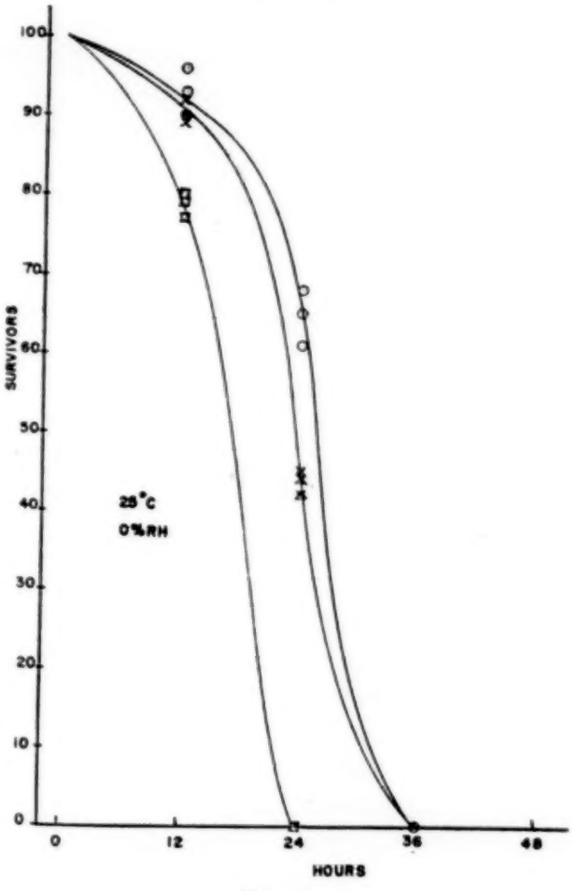

FIG. 9.

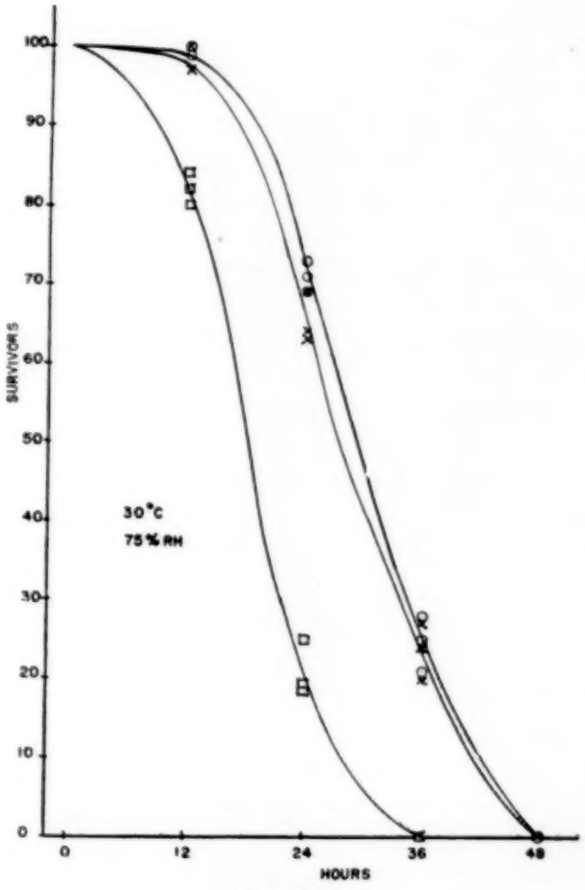

FIG. 11.

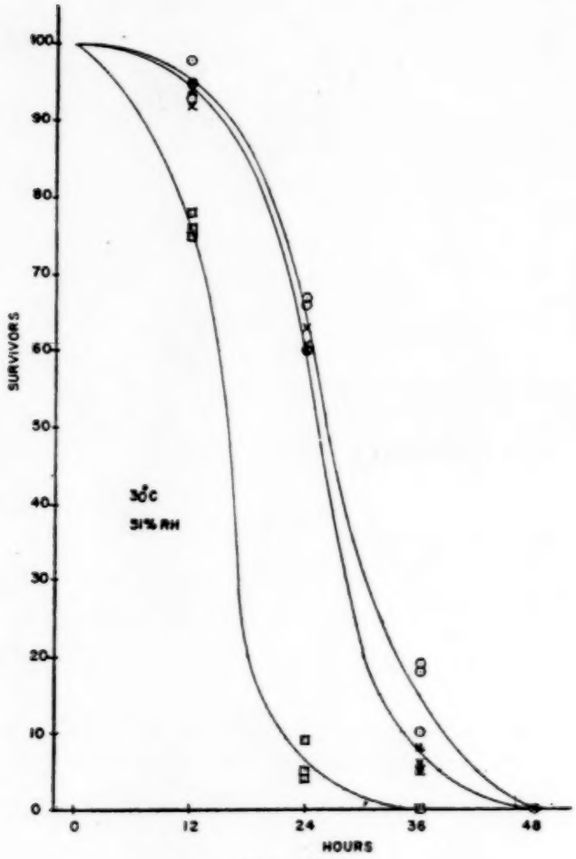

FIG. 12.

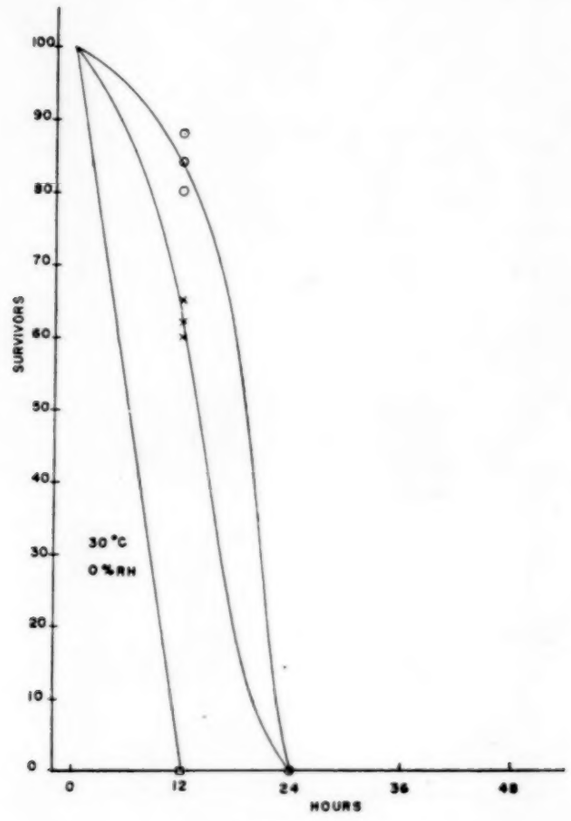

FIG. 14.

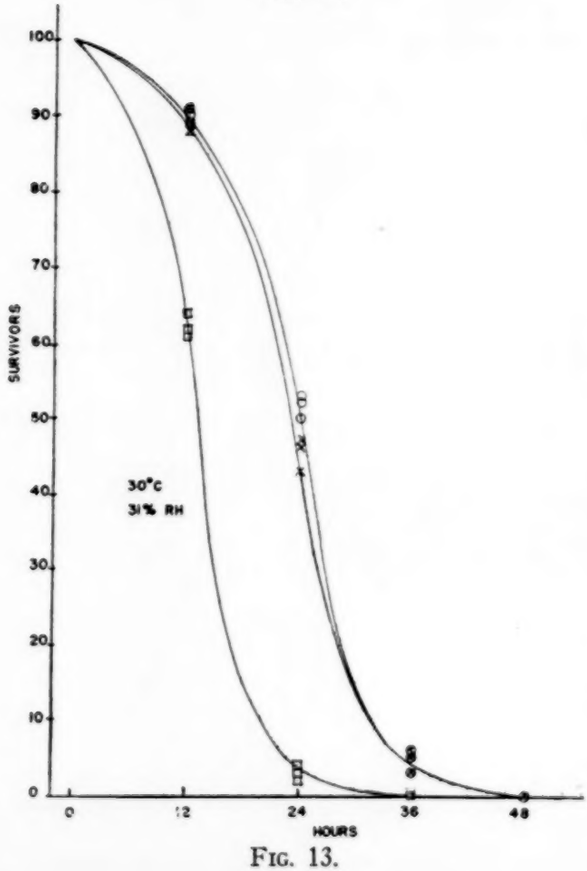

FIG. 13.

show that ST/ST is always the superior chromosome type in terms of adult survival regardless of the relative humidity. As the relative humidity decreases death rate becomes more rapid for all the chromosome types, but that of CH/CH is always the highest. Clearly, carriers of the ST/ST homozygotes are better adapted to 25° C. at all of the relative humidities tested than CH/CH. The heterozygote on the other hand is intermediate in survival at 25° C. and all of the relative humidities tested except 100% relative humidity where it is the same as ST/ST. At 30° C. ST/CH is not significantly different from ST/ST at all of the relative humidities tested. CH/CH at this temperature has a higher death rate than ST/ST and ST/CH. The greater survival of ST/ST and ST/CH at 30° C. would indicate that at the higher temperatures they are better adapted than CH/CH.

From the higher death rate of CH/CH adults it can be concluded therefore, that they are less adapted to temperatures of 25° C. and above regardless of the relative humidity. Also it can be concluded that temperature and humidity are among the environmental factors bringing about the differential survival of adults of the three chromosome types at Piñon Flat by acting on the pupal and adult stages.

Discussion and Conclusions

Clear evaluation of the effects in nature of the environmental factors studied here must await further knowledge of the feeding and breeding sites at Piñon Flat. Until this is at hand we can only assume that these are not dissimilar to those which Carson (1951) has described at Mather, in the central Sierra Nevada, and that the activities of the flies at different stages of their life cycle are similar at both sites. This being true, it would appear that the eggs are laid in a fluid or semi-fluid medium in which the larvae develop and that the pupae are formed at the margin of the medium. These stages would accordingly respond more or less directly to conditions of temperature but would be affected by the atmospheric humidity only to the extent that it affects the slime flux, concentrating it or drying it. The adult stage would respond more directly to both the air temperature and its relative humidity. These facts must be borne in mind in any attempt to evaluate the results of laboratory experiments.

The effect of temperature cannot be readily distinguished from that of desiccation at relatively low humidities. At 30° C. pupae survived only when the relative humidity was 76% or more; the longevity of adults was found to increase at 25° C. and 30° C. when the relative humidity increased (tables 5 and 6). The extent to which the limits set forth in these tables are actually effective in nature is as yet difficult if not impossible to state. Air temperatures may rise to 38° C. or more and may continue above 30° C. for several hours. The relative humidity may continue during the same period as low as 20–40%. These conditions would appear to be fatal. Yet the population is apparently able to survive them, presumably because the conditions to which it is actually subjected are much less severe. Furthermore, it may remain quiescent under these conditions, for Mitchell and Epling (1951) have shown that flight activity of adults, at least as measured by feeding at baited traps, occurs chiefly during brief periods shortly after sunrise and before sunset.

Pupae, on the other hand, because they are immobile, will be more likely to be affected by temperature and relative humidity conditions. The conditions prevailing at the time of pupation are of great importance, for the early pupal case has not hardened and, like the larva, cannot withstand much evaporation. In the slime fluxes at Mather, California, larvae of *D. pseudoobscura* pupate in the moist flux substrate, and unless the flux begins to dry up, metamorphosis will be completed under an almost saturated relative humidity. If, however, the flux does begin to dry out before eclosion, then the viability of the pupae will decrease.

Finally, the factor of larval and adult nutrition plays an important role in maintaining the fly populations. Perhaps the great decrease in overall adult population size at Piñon Flat in the summer is due to the shortage of yeast and other microorganisms used as food brought about by the desiccation of the fluxes on which this microflora grows. In addition to the quantity of food available to larvae and adults of *D. pseudoobscura* its quality may also be important. Wagner (1944 and 1949) has shown that the yeasts available in nature to the larvae of *D. aldrichi* are not always the optimum for growth and development. Little is known about the relationship between adults in nature and the wild yeasts, although da Cunha, Dobzhansky, and Sokoloff (1951) have shown that adults of different species of *Drosophila* are attracted differ-

ently by different yeasts placed in traps in the field at Mather, California. Buzzati-Traverso (personal communication) has shown that a similar reaction occurs for *D. subobscura* when released within a closed space and retrieved from different yeast cultures. It is also known that the quality and quantity of yeasts available to adults affects the viability of eggs of *D. melanogaster*. Similarly, larval nutrition has an effect on pupal and adult mortality of this species (Sang, 1950). The role of nutrition in the Piñon Flat populations of *D. pseudoobscura* can be studied more completely when the feeding sites of the larvae and adults are known.

Until Heuts (1947) experimented with humidity and the pupal viability of some third chromosome types from Piñon Flat there was little evidence for the causes of adaptive differences between the chromosome types. Accordingly an attempt was made by the present author to determine the nature and extent of adaptive differences, if any, between the ST/ST, ST/CH, and CH/CH chromosome types from Piñon Flat. The responses of the different chromosome types in terms of their viability, growth, and longevity have accordingly been emphasized in this paper.

The experiments recorded here which concern the effect of temperature on egg viability and hatching rate and of temperature and nutrition on larval growth rate and viability gave purely negative results. No differences between the ST/ST, ST/CH, and CH/CH chromosome types were found. Differences of relative humidity and temperature were shown, on the other hand, to affect pupal viability and adult longevity. ST/ST pupae are better adapted to low relative humidities than are ST/CH and CH/CH pupae. ST/CH pupae are intermediate in viability. Adults of the ST/ST and ST/CH chromosome types live longer than CH/CH at several relative humidities at both 25° C. and 30° C. In general, ST/CH adults are intermediate in the longevity except at 30° C. where they have the same longevity as the ST/ST adults. Thus, it has been clearly shown that there is differential adaptedness during the pupal and adult stages for the carriers of ST and CH chromosomes. What do these findings mean in terms of the chromosome cycle in Piñon Flat populations? The frequency of ST chromosomes is high in March, then it drops until, during June, it is lower than CH, but in July its frequency increases markedly and there is further increase during August, September, and October. During the summer months the size of the whole fly population decreases markedly. Perhaps this is due to the drying up of the feeding and breeding sites because of the relatively high temperature and low atmospheric relative humidity. No flies have been caught during the winter months; the earliest collecting possible has been in March. During this month the temperature is mild and the relative humidity is high; the frequency of ST chromosomes is relatively high. The carriers of these chromosomes are believed to have persisted during the winter months.

The results obtained here indicate that ST chromosomes increase in summer, relative to CH chromosomes, at least in part, because of the greater adaptedness of their pupal and adult carriers to the conditions of temperature and humidity prevailing at this time. They show also that the ST carriers are as well adapted as CH to the high relative humidities which prevail during the late fall, winter and early spring months. They explain in part how the seasonal cycle observed at Piñon Flat may come about, that is, by elimination of CH carriers. They throw no light on the greater adaptedness of the carriers of CH chromosomes to the conditions of early summer and their consequent increase during this period, nor do they explain the observed superiority of ST/CH heterozygotes in population cages at 25° C.

The only indication that the carriers of

CH chromosomes may be superior under some conditions to ST carriers is the information reported on pupal viability, where it was shown that although less viable than ST, CH was more viable than the heterozygote at 25° C. and 76% R. H. This experiment was repeated three times, and the results were consistently the same. A certain combination of factors may according exist at Piñon Flat during the early summer which result in the increase of CH types. But what this may be remains unknown.

The increased frequency of ST/CH heterozygotes in population cages above that expected on the basis of the Hardy-Weinberg formula, is of great importance since it leads to a consideration of adaptedness and heterosis. According to Dobzhansky (1950) "variations in the gene arrangements in chromosomes of natural populations are often, and perhaps always, connected with the maintenance of heterosis." Inversion heterozygotes have been found to have adaptive superiority to homozygotes in *D. pseudoobscura* by Dobzhansky (1943, 1947a, b, 1949), Wright and Dobzhansky (1946), and Dobzhansky and Levene (1948). These authors have found that inversion heterozygotes in which both chromosomes involved come from the same locality, such as Piñon Flat, occur in higher frequency in artificial populations in population cages than would be expected if selection were acting randomly on homozygotes and the heterozygotes alike. Similar evidence has been obtained by Dubinin and Tiniakov (1945) for *D. funebris,* by Carson and Stalker (1947) and Levitan (1951) for *D. robusta,* and by Spiess (1950) for *D. persimilis.*

It is clear that the cycle at Piñon Flat is due to natural selection (see Dobzhansky, 1947a, and Dobzhansky and Levene, 1948) of genotypes which are best adapted to the hotter and drier conditions of late summer and early autumn, aided by the presence of inversions in the third chromosome. Pairing is not normal in an inversion heterozygote such as ST/CH, and crossing over is reduced to a small fraction of the normal rate (Dobzhansky and Epling, 1948). Because of this, the inversion acts as a gene block, and maintains particular constellations of genes in the population, barring mutation and new spontaneous chromosome rearrangements. The heterosis or superior adaptedness of the Piñon ST/CH heterozygote is produced according to Dobzhansky (1950) by an "interaction of polygene complexes which have become coadapted by natural selection in the course of evolutionary progress." It would seem, therefore, that the type of experiments presented here might throw some light on the adaptive superiority of the ST/CH heterozygote. Nevertheless, the heterozygote was not more viable, nor longer lived in the pupal and adult stages, but was intermediate between the two homozygotes, with two exceptions. One has been referred to in a preceding paragraph. The other was a case of adult longevity when ST/CH was found to be the same as ST/CH at 25° C. and 100% relative humidity and at 30° C. at all of the relative humidities tested.

The absence of experimental evidence for the adaptive superiority or the heterosis of ST/CH may be due, in part, to the nature of the experiments presented here, for they differ in one important way from the cage experiments of Dobzhansky and others, namely in the absence of competition between the chromosome types during the various stages of the life cycle. A series of experiments is planned, however, which will test the adaptive responses of ST/ST, ST/CH, and CH/CH when the three types are in competition with each other during the larval stage.

The data presented in this paper show that three third chromosome types, ST/ST, ST/CH, and CH/CH from Piñon Flat respond differently to temperature and relative humidity primarily in the pupal and adult stages. However, it cannot be concluded that these differences in response are the complete basis

for the cyclic change in the frequency of ST and CH chromosomes. The final conclusions will depend upon the finding and analysis of the climatic conditions there.

Acknowledgments

The author wishes to express his gratitude to Professors Carl Epling and Curt Stern under whose guidance this work was done. The advice of Professor Lennart Johnson concerning the statistical treatment of the data is appreciated.

Summary

An attempt has been made to determine the causes for the differential adaptedness of the ST/ST, ST/CH, and CH/CH chromosome types from Piñon Flat in the San Jacinto Mountains of southern California. The effects of temperature, nutrition, and relative humidity on the egg, larval, pupal, and adult stages were investigated. The following results were obtained:

1. Egg viability and egg hatching rate are the same for the ST/ST, ST/CH, and CH/CH chromosome types at 15° C., 25° C., and 30° C.

2. The viability of the larvae of the three chromosome types is the same at 15°, 25°, and 30° C. (30° C. was found to be sublethal.) Larval growth rates were found to be the same for each type. They were determined by the duration of the larval stage fed on several wild yeasts.

3. At 25° C., ST/ST pupae are more viable than ST/CH and CH/CH pupae at relative humidities of 76% and below. ST/CH was found to be more viable than CH/CH at 56% relative humidity and lower. Pupal viability is the same at 100% and 92% relative humidity contrary to the results obtained by Heuts. 30° C. was found to be lethal for the three chromosome types at relative humidities of 75% and lower. At 100% and 92% relative humidity at this temperature, the viability of the three chromosome types was found to be equal. The differences of pupal viability shown by the three chromosome types at 25° C. and relative humidities of 76% and lower were found to be statistically significant ($P < 0.01$).

4. Adults of ST/ST and ST/CH live longer than do CH/CH adults at 25° and 30° C. at several different relative humidities. At 25° C. ST/CH adults are intermediate in survival except at 100% relative humidity where they are similar to ST/ST. At 30° C. ST/CH is similar to ST/ST at all of the humidities tested.

5. The general conclusion is that the experimental evidence indicates that the differential adaptedness of the three chromosome types of Piñon Flat flies is effective at least in part, during the pupal and adult stages.

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GENETICS OF NATURAL POPULATIONS. XX. CHANGES INDUCED BY DROUGHT IN *DROSOPHILA PSEUDOOBSCURA* AND *DROSOPHILA PERSIMILIS*[1]

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INTRODUCTION

Although evolutionary changes are mostly too slow to be observed within a human lifetime, cases of genetic alterations in populations of various organisms have been reported in recent years. Naturally enough, most of these changes have been observed either in microorganisms, or in species directly influenced by human activities. Changes in higher organisms in which man is not a causative agent are of two kinds. Cyclic seasonal changes are known in several species of *Drosophila,* in the beetle, *Adalia bipunctata,* in the hamster, *Cricetus cricetus,* and in some others (Timofeeff-Ressovsky, 1940; Gershenson, 1945; Dobzhansky, 1948; and others). Trends of change which persist for several years are also recorded. The most widely known trend of this sort involves the development of melanism in industrial regions in several species of moths. Ford (1937, 1945) interprets the spread of industrial melanism as a result of release of the selection pressure which discriminates against the melanic mutants in non-industrial territories. Dobzhansky (1947) has reported a change in the incidence of chromosomal variants in a population of *Drosophila pseudoobscura* in the population of Keen Camp, in California, between 1939 and 1946. Finally, Fisher and Ford (1947) have described a change in the population of the moth, *Panaxia dominula,* in a locality in England, which involves an increase of the incidence of a certain genotype between 1929 and 1939, and a decrease of the same genotype thereafter. Neither Dobzhansky nor Fisher and Ford were able to discern the causes which brought about the changes which they recorded.

The present article describes observations on the populations of *Drosophila pseudoobscura* and *Drosophila persimilis* at Mather, in the Sierra Nevada of California (some 350 miles from Keen Camp). Changes in these populations have been observed between 1945 and 1951. It is probable, although not fully established, that these changes were induced by the cumulative effects of a succession of dry years during this period.

MATERIAL

The flies which served as material for this study were collected at Mather and in adjacent localities in the summers of 1945, 1946, 1947, 1950, and 1951. Cups with fermenting banana were used to attract the flies, except in a few cases where larger containers were used (see below). The cytological examinations were made mostly in the field laboratory at Mather, but some flies were sent to the laboratory in New York. Wild females were placed singly in bottles with the cornmeal-molasses, or with the cream of wheat-molasses, medium. Chromosomes were studied in a single larva from the progeny of each female. All the determinations of the gene arrangements were made by the writer.

GENE ARRANGEMENTS IN THE MATHER POPULATION OF *Drosophila Pseudoobscura*

Seven gene arrangements occur in the third chromosomes of the Mather population of *D. pseudoobscura.* Two of them,

[1] The final stages of the work reported here were done under Contract No. AT-(30-1)-1151, U. S. Atomic Energy Commission.

TABLE 1. *Frequencies (in per cent) of the gene arrangements in the Mather population of* Drosophila pseudoobscura. ST—Standard; AR—Arrowhead: CH—Chiricahua; TL—Tree Line; PP—Pikes Peak; SC—Santa Cruz; OL—Olympic; n—Number of chromosomes studied

Month	Year	ST	AR	CH	TL	PP	SC	OL	n
May	1947	25.7	47.1	18.6	4.3	—	—	4.3	140
June	1946	21.9	42.7	20.2	11.2	0.6	1.7	1.7	178
	1947	29.5	42.6	19.7	5.7	—	1.6	0.8	122
	1950	16.1	57.8	15.0	8.9	1.1	0.6	0.6	180
	1951	27.0	47.0	12.0	7.0	2.0	2.0	3.0	100
	Total	22.6	48.1	17.1	8.6	0.9	1.4	1.4	580
July	1945	35.7	35.7	17.2	10.4	—	0.6	0.3	380
	1947	30.3	38.2	20.4	8.2	1.0	1.6	0.3	304
	1950	19.8	55.7	16.0	4.7	3.8	—	—	106
	1951	29.3	46.2	10.8	8.2	3.8	1.0	0.7	416
	Total	30.4	42.1	15.6	8.5	2.0	1.0	0.4	1,134
August	1946	39.9	30.4	13.9	10.1	—	3.2	2.5	158
	1950	21.9	45.8	18.4	9.5	3.2	1.0	0.2	526
	1951	29.7	38.5	11.5	12.1	6.2	1.2	0.9	340
	Total	27.2	41.0	15.4	10.4	3.7	1.4	0.8	1,024
Sept.	1947	35.8	31.2	20.8	7.5	0.8	3.3	0.4	240
Grand Total									3,118

namely, Arrowhead (AR) and Standard (ST) are very common; two others, Chiricahua (CH) and Tree Line (TL), are moderately frequent; and three, Pikes Peak (PP), Santa Cruz (SC), and Olympic (OL), are rare. Of course, some of the wild flies carry two chromosomes with the same gene arrangement (structural homozygotes), and others have two chromosomes with different gene arrangements (structural heterozygotes).

A summary of the data on the relative frequencies of the gene arrangements is presented in table 1. The data for 1945–1947 have been published in Dobzhansky, 1948. It is clear at a glance that the frequencies of some of the gene arrangements undergo cyclic seasonal changes and are often different in successive months. Thus, ST chromosomes are relatively rare in May and June and more frequent in the latter part of the summer. To test the statistical validity of these changes, the chromosomes are divided into two classes, those with ST and those with gene arrangements other than ST. The chi-square for the monthly totals turns out to be 19.12, which, for 4 degrees of freedom, has a probability of chance occurrence of about 0.001. The changes in AR chromosomes are the converse of those in ST: the frequencies of AR decrease from 47–48 per cent in May and June to about 40 per cent in late summer. The chi-square for AR chromosomes is 21.74, which may occur by chance less than once in one thousand trials. No significant changes in frequencies in different months are found for CH and TL chromosomes (chi-squares 5.38 and 7.16, probabilities of chance occurrence about 0.25 and 0.13, respectively). Among the rare gene arrangements, only PP appears to undergo changes in frequency with season, but this arrangement was too infrequent before 1950 to enable us to judge the cyclic nature of the changes recorded. If the chromosomes listed in table 1 are divided into three classes, namely, ST, AR, and "others," the joint chi-square for homogeneity on different months becomes 30.64. For 8 degrees

of freedom, this has a probability of chance occurrence less than 0.001.

The changes so far analyzed are cyclic, and they have apparently recurred in every year for which at least two observations are available (1946, 1947, 1950, and 1951). Further consideration of the data in Table 1 discloses that the composition of the Mather population was significantly different during the same season in different years. Starting with 1945, the frequencies of ST chromosomes were decreasing, and those of AR were increasing, until the former reached minimal and the latter maximal frequencies in 1950 (unfortunately, no data are available for 1948 and 1949). In 1951, ST chromosomes were again more common, and AR were less frequent, than they were on corresponding months in 1950. No definite trends are apparent for CH and TL chromosomes; if anything, the CH chromosomes were becoming less frequent during the period of observation. A very clear gain has, however, been observed in PP chromosomes. The PP gene arrangement was not encountered at all at Mather in 1945; in 1946 a single chromosome was recorded; in 1947 several chromosomes were found; in 1950, and especially in 1951, PP chromosomes were found regularly in all samples, and their frequency reached 6.2 per cent in August of 1951.

To test the statistical validity of the changes from year to year, the chromosomes are again divided into three classes: ST, AR, and "others." Since seasonal changes are known to occur, the analysis for the changes from year to year must be made separately for each month. The chi-squares obtained are as follows:

Month	Chi-Square	Degrees of freedom	Probability
June	16.02	6	0.01
July	20.31	6	0.003
August	23.50	4	<0.001

The Gene Arrangements in the *Drosophila Pseudoobscura* Populations of the Sierran Transect

The Mather locality lies at an elevation of 4,600–4,700 feet on the western slope of the Sierra Nevada of California. Dobzhansky (1948) has taken samples of the populations of several other localities in the same region, ranging in elevation from 850 to 10,500 feet and forming a rough west-east transect across the Sierra Nevada mountain system. Examination of the frequencies of the gene arrangements in the third chromosomes in these populations showed that ST chromosomes become progressively less frequent, and AR chromosomes more frequent, with increasing elevation. Seasonal changes in the frequencies of ST and AR chromosomes were observed in 1947 at Lost Claim Camp (elevation about 3,000 feet) and at Aspen Ranger Station (elevation 6,200 feet). These changes have the same character as described for Mather, i.e., the frequencies of ST increase and those of AR dwindle with season.

On July 13–17, 1951, a sample of 152 third chromosomes was taken at the Aspen Ranger Station, and on August 18–19, 1951, a sample of 28 third chromosomes was obtained on Porcupine Flat (elevation 8,000 feet). The observed frequencies of the gene arrangement are shown in Table 2:

Table 2. *Frequencies (in per cent) of the gene arrangements in the Aspen and Porcupine populations of* Drosophila pseudoobscura
The abbreviations are the same as in Table 1

Locality	ST	AR	CH	TL	PP	OL	n
Aspen	21.1	52.6	13.2	5.9	6.6	0.7	152
Porcupine	7.1	60.7	21.5	3.6	7.1	—	28

Comparison of the data in tables 1 and 2 shows that, in July and August of 1951, ST chromosomes were most frequent at Mather, less so at Aspen, and least at

Porcupine. Conversely, AR chromosomes were most frequent at Porcupine, less so at Aspen, and least at Mather. This confirms the existence of the altitudinal gradients in the frequencies of ST and AR chromosomes recorded by Dobzhansky (1948). Whether the genetic changes which took place in the composition of the Mather population between the years 1945 and 1951 occurred also at Aspen and at Porcupine is uncertain. The data are suggestive only with respect to the PP gene arrangement, which, as shown above, increased in frequency at Mather during the above period. Only a single PP chromosome was found among the 478 third chromosomes examined from Aspen in 1946 and 1947. None were found among the 38 chromosomes from Porcupine taken on the same year. Yet, in 1951 the PP chromosomes constituted 6–7 per cent of the samples from these localities. It appears that the PP gene arrangement was gaining ground in the Sierran populations.

The Gene Arrangements in the Mather Populations of *Drosophila Persimilis*

Drosophila persimilis is a species closely related to *D. pseudoobscura* and yet maintaining its identity in mixed populations with the latter (cf. Dobzhansky, 1951, and other work). Five gene arrangements occur in the third chromosomes of the Mather population (not counting a sixth which has been seen only once and may conceivably represent a recently arisen mutant). These are Whitney (WH), Standard (ST), identical with the ST of *D. pseudoobscura,* Klamath (KL), Mendocino (MD), and Sequoia (SE). In contrast to *D. pseudoobscura,* no significant seasonal changes in the incidence of the gene arrangements have been observed in *D. persimilis* (Dobzhansky, 1948, and more recent data). It is, therefore, legitimate to group the data by the year (or, rather, summer) of collecting. Table 3 presents the data in this form.

It can be seen that the incidence of WH chromosomes in the population rose from a minimum in 1945 to a maximum in 1950, but fell again in 1951 to almost the 1945 level. The converse happened with the ST and KL chromosomes, the frequency of which decreased between 1945 and 1950, and rose again in 1951. MD and SE remained rare throughout and showed no consistent changes. To test the statistical significance of the observed changes, the chromosomes were divided into four classes: WH, ST, KL, and "others." The chi-square computed from the data is 42.36. For 12 degrees of freedom the probability of such or greater value is much less than 0.001. One may also divide the chromosomes in two groups: those with the WH gene arrangements and "others." The chi-square then turns out 23.96, which for 4 degrees of freedom has a probability less than 0.001. The changes observed from year to year are quite significant.

Table 3. *Frequencies (in per cent) of the gene arrangements in the Mather populations of* Drosophila persimilis. WH—Whitney; KL—Klamath; MD—Mendocino; SE—Sequoia; n—Number of chromosomes studied

Year	WH	ST	KL	MD	SE	Others	n
1945	69.7	8.6	15.2	6.1	0.5	—	198
1946	76.6	10.9	10.2	1.6	0.8	—	128
1947	79.5	8.3	6.9	4.8	0.2	0.2	434
1950	87.1	4.9	5.4	2.2	0.4	—	224
1951	72.1	10.3	15.4	1.8	0.4	—	272
Total	77.4	8.4	10.1	3.6	0.4	0.1	1,256

TABLE 4. *Frequencies (in per cent) of the gene arrangements in the Aspen and Porcupine populations of* Drosophila persimilis

The abbreviations are the same as in table 3

Locality and year	WH	ST	KL	MD	SE	n
Aspen, 1946	68.5	11.1	14.8	5.6	—	108
Aspen, 1947	81.3	9.2	5.3	4.2	—	262
Aspen, 1951	87.5	2.5	7.5	2.5	—	40
Aspen, Total	78.5	9.0	8.0	4.4	—	410
Porcupine, 1946	76.8	11.0	7.3	4.9	—	82
Porcupine, 1947	85.1	9.1	2.5	2.5	0.8	121
Porcupine, 1951	96.7	—	2.2	1.1	—	92
Porcupine, Total	86.4	6.8	3.7	2.7	0.3	295

THE GENE ARRANGEMENTS IN THE *Drosophila persimilis* POPULATIONS OF THE SIERRAN TRANSECT

Like those of *Drosophila pseudoobscura,* the populations of *D. persimilis* show altitudinal gradients in the frequencies of the gene arrangements at different elevations. Namely, the WH chromosomes become progressively more frequent as one ascends the slope of the Sierra, while ST, KL, and MD are appreciably more common at low than they are at high elevations (Dobzhansky, 1948). The results of the samplings of the populations of Aspen Ranger Station and of Porcupine Flat are summarized in table 4.

It can be seen that the Aspen and Porcupine Flat populations suffered the same changes which occurred in the Mather population between 1945 and 1951. The frequencies of WH chromosomes have risen and those of the other gene arrangements have fallen with time. Unfortunately, no samples have been taken between 1948 and 1950, and it is consequently unknown whether the 1951 frequency of WH chromosomes is or is not lower than it was in 1950, as observed at Mather. Statistically, the reality of the changes is assured. Dividing the chromosomes into two classes, those with WH and with "other" gene arrangements, the chi-squares for the Aspen and Porcupine populations are 10.10 and

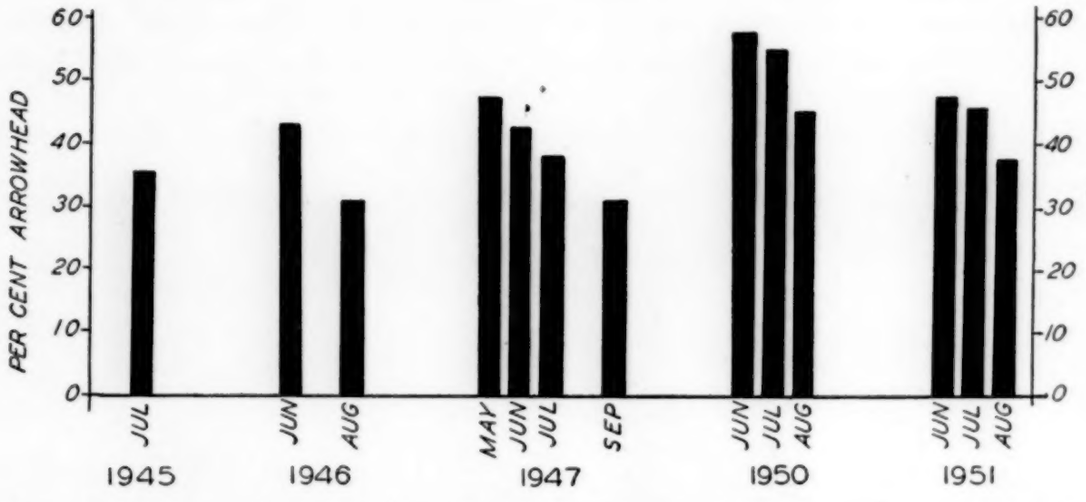

FIG. 1. The frequencies of the Arrowhead gene arrangement in *Drosophila pseudoobscura* at Mather, California.

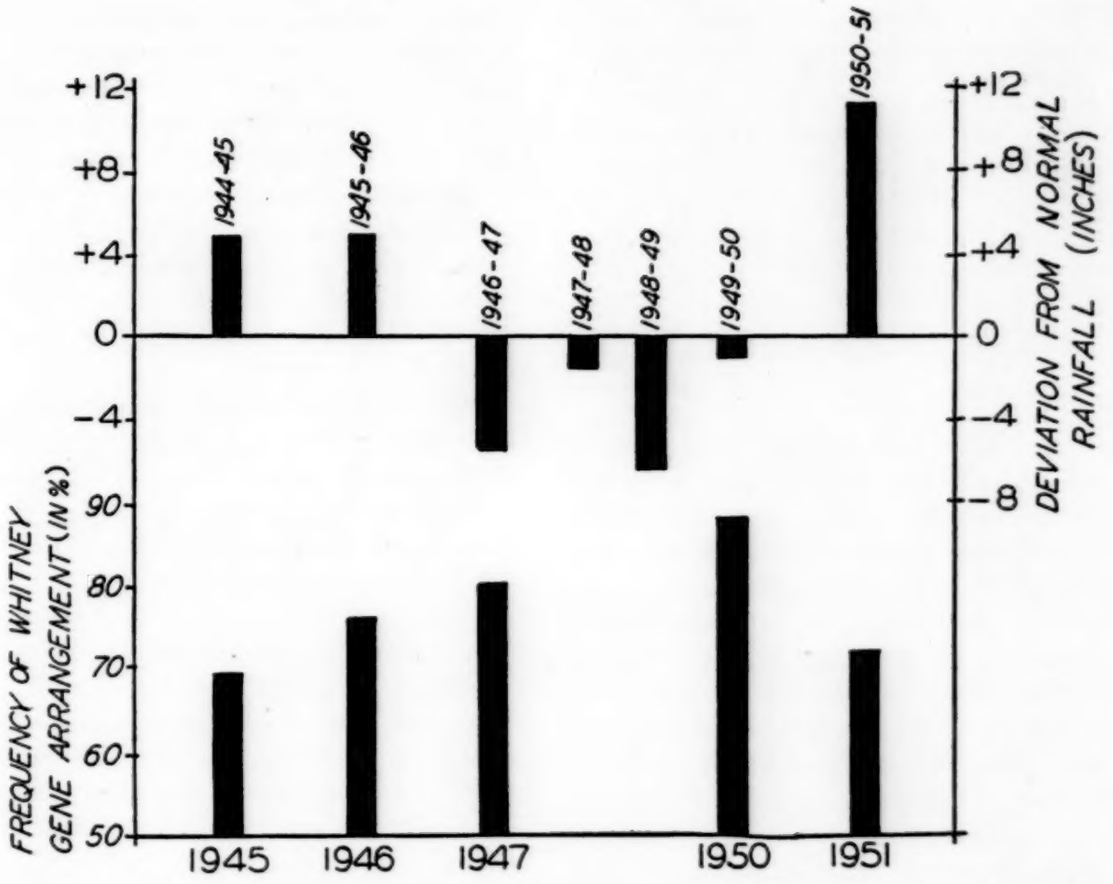

FIG. 2. The frequencies of the Whitney gene arrangement in *Drosophila persimilis* at Mather, and the deviations from the normal amounts of precipitation observed at Yosemite Park Headquarters, in California.

31.92, respectively. For 2 degrees of freedom the probability of chance occurrence of such values is less than 0.01.

POSSIBLE CORRELATIONS WITH THE CLIMATE CHANGES

It has been shown that the two species, *Drosophila pseudoobscura* and *D. persimilis,* were undergoing parallel changes in the genetic composition of their populations in the Yosemite Park region of the Sierra Nevada of California. At Mather, the ST chromosomes in *D. pseudoobscura* fell in frequency between 1945 and 1950 and recovered some of the lost ground in 1951. AR chromosomes changed in the direction opposite to ST. PP chromosomes reached their maximum frequency in 1951. In *D. persimilis* the incidence of WH chromosomes rose and of ST and KL chromosomes fell in the Mather population between 1945 and 1950, a partial reversal of the change taking place in 1951. The *D. persimilis* populations of the neighboring localities, Aspen and Porcupine, suffered apparently the same changes as did the population of Mather. Whether the changes in *D. pseudoobscura* were also parallel in the three localities is not clear but it seems probable.

The situation is clearly one which suggests that most of the changes observed had a common cause, and the experience gained in studying the Sierran populations during five summers points to the increasing aridity as a possible factor. The Transition Life Zone of the Sierra Nevada is characterized by almost rainless summers, and by relatively abundant precipitation, both in the form of rain and snow, from November to April. The amount of precipitation received during winter determines the ground water level

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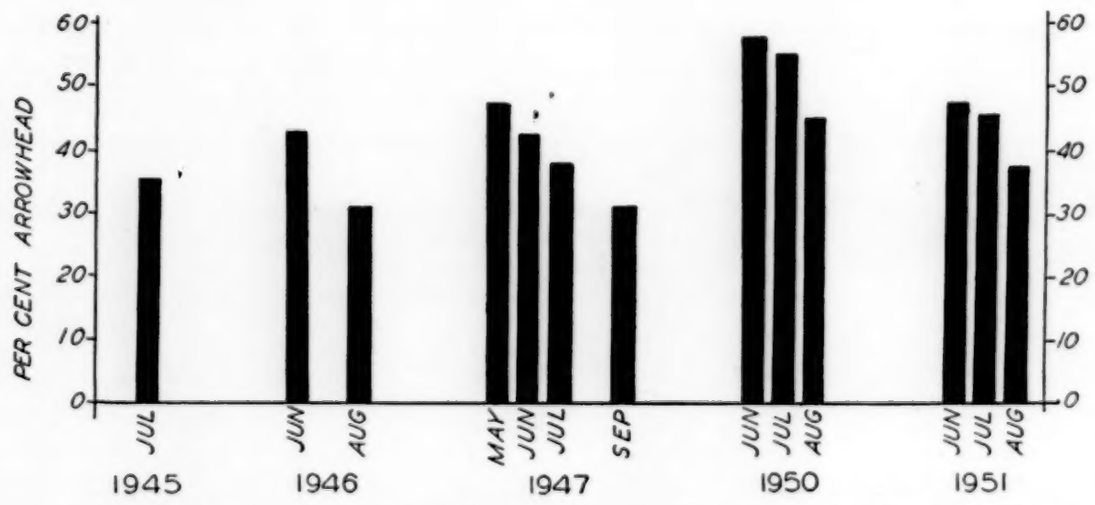

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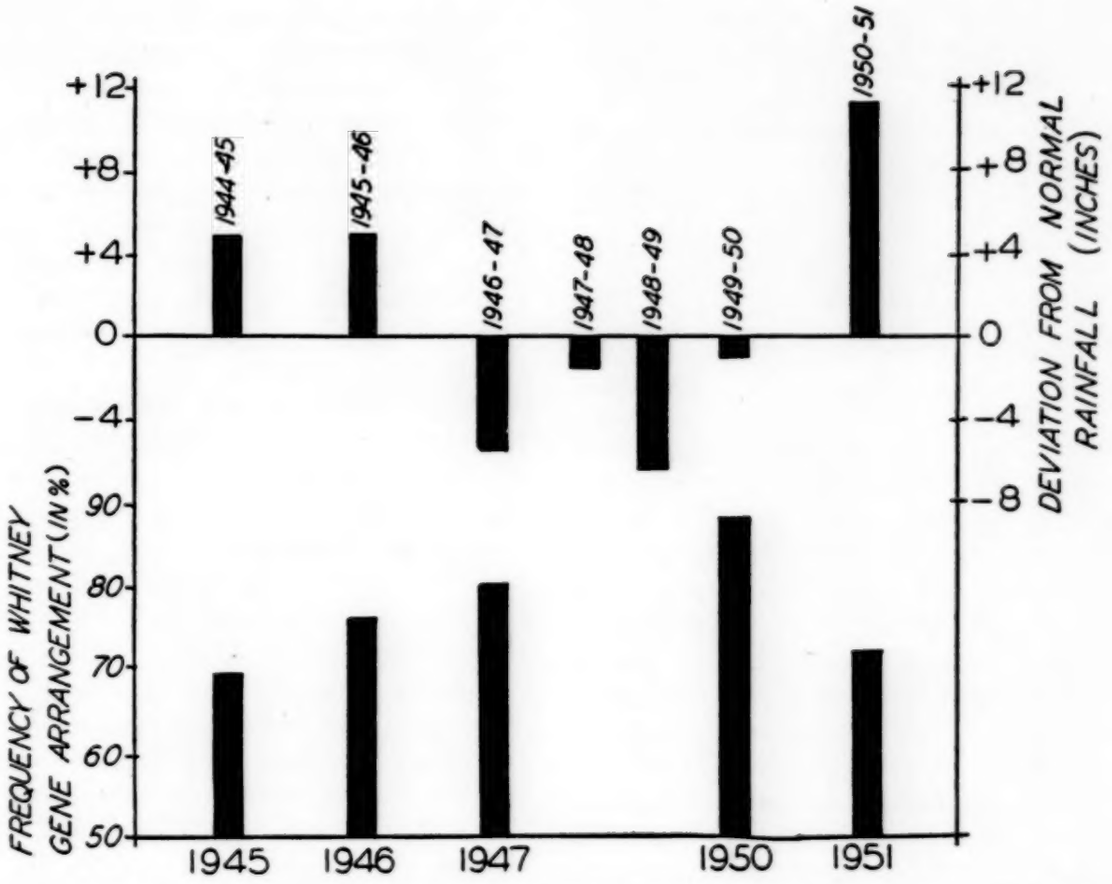

FIG. 2. The frequencies of the Whitney gene arrangement in *Drosophila persimilis* at Mather, and the deviations from the normal amounts of precipitation observed at Yosemite Park Headquarters, in California.

31.92, respectively. For 2 degrees of freedom the probability of chance occurrence of such values is less than 0.01.

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The situation is clearly one which suggests that most of the changes observed had a common cause, and the experience gained in studying the Sierran populations during five summers points to the increasing aridity as a possible factor. The Transition Life Zone of the Sierra Nevada is characterized by almost rainless summers, and by relatively abundant precipitation, both in the form of rain and snow, from November to April. The amount of precipitation received during winter determines the ground water level

TABLE 5. *The deviation (in inches) from the normal amounts of precipitation observed in various years at the Hetch-Hetchy and the Yosemite Park Meteorological Stations*

Year	Hetch-Hetchy	Yosemite Park
1945–1946	+2.57	+4.93
1946–1947	−6.38	−5.36
1947–1948	−1.47	−1.14
1948–1949	−8.69	−6.19
1949–1950	−4.56	−0.72
1950–1951	+15.11	+11.25

and the welfare of the vegetation, as well as of much of the animal life, during the summer months. Dr. W. M. Hiesey has very generously furnished the data on the mean precipitation and mean temperature recorded at Hetch-Hetchy (about 5 miles north of Mather) and at the Yosemite National Park headquarters (about 17 miles southeast of Mather) as copied by him in the office of the U. S. Weather Bureau in San Francisco. Table 5 shows the deviations from the normal (average) precipitation records observed between July of the preceding and June of the succeeding year.

The precipitation was deficient in the Yosemite Park region between 1946 and 1950, which is the period during which the *Drosophila* populations suffered the changes reported above. The winter of 1950 was, however, very wet, and, although the spring months of 1951 were again drier and warmer than normal, the early summer of 1951 at Mather showed every indication of abundant water supply in the soil. The *Drosophila* populations have in the summer of 1951 largely restored the genetic composition which they had in 1945–1946.

RELATIVE FREQUENCIES OF SPECIES IN THE MATHER POPULATION

The changing environmental pressures on populations of ecologically similar species may manifest themselves in variations of the relative abundance of these species in a locality. This is the consequence of the fact that sympatric species, even ecologically parallel ones, exploit the environment in somewhat different ways. Three species of the *obscura* group, namely, *Drosophila pseudoobscura, D. persimilis,* and *D. azteca,* occur at Mather. Their females are difficult to distinguish in making mass classifications; males of *azteca* can, however, be easily separated from the other two species. Table 6 summarizes the data for the Mather samples.

Table 6 shows that *D. azteca* increases in relative frequency in the population as the season progresses. The changes are surprisingly regular; except for a very high frequency in September of 1947, no appreciable variations from year to year are recorded. At elevations higher than that of Mather (4,700 feet), *D. azteca* becomes rare or absent. At Porcupine Flat (8,000 feet), a single male of this species was identified in August of 1951 among several hundred males of *D. pseudoobscura* and *D. persimilis.* At Aspen (6,200 feet), *D. azteca* is less

TABLE 6. *Frequency of* Drosophila azteca, *in per cent of the males belonging to this species in samples containing* D. azteca, D. pseudoobscura, *and* D. persimilis, *at Mather, California*

Time of collecting	Males classified	Per cent *azteca*
June 8–15, 1945	547	36
August 10, 1945	167	39
August 22–September 5, 1945	1,134	50
June 4–15, 1946	718	18
June 26–30, 1946	201	30
August 9–10, 1946	227	45
June 22–26, 1947	188	12
July 26, 1947	584	34
September 1–4, 1947	1,139	77
September 12, 1947	393	68
June 29, 1950	314	32
July 25–28, 1950	285	35
August 18–27, 1950	890	42
June 25, 1951	87	33
July 6–19, 1951	481	25
August 10–26, 1951	407	43

TABLE 7. *Percentages of* Drosophila persimilis *in samples from Mather containing the species named and* D. pseudoobscura

Time of collecting	Strains examined	Per cent *persimilis*
July 8–15, 1945	155	37
August 22–September 5, 1945	543	40
June 4–15, 1946	2,065	34
August 9–10, 1946	79	29
May 15, 1947	59	41
June 22–26, 1947	100	39
July 5, 1947	66	21
July 26, 1947	116	14
September 1–12, 1947	110	45
June 29, 1950	68	30
July 25–28, 1950	57	30
August 18–27, 1950	141	51
June 26–30, 1951	56	11
July 1–15, 1951	132	11
July 16–30, 1951	57	5
August 7–16, 1951	38	3

common than at Mather, but it shows the same increase in relative abundance towards the end of the season.

D. persimilis can be distinguished from *D. pseudoobscura* either by outcrossing wild flies or their offspring to known representatives of the sibling species (genetic method), or by examination of the chromosomes in salivary gland preparations (cytological method), or by examination of the male genitalia as indicated by Rizki (1951). The first two methods have been used for classification of the samples from Mather. The results are summarized in table 7.

The relative frequencies of *D. pseudoobscura* and *D. persimilis* oscillate rather irregularly. In 1947, but apparently not in 1950, frequency of *D. persimilis* declined with the season. Most remarkable, however, is the almost catastrophic drop which *D. persimilis* has suffered in 1951, after having maintained a rather constant incidence from 1945 till 1950. This behavior parallels neither the known climatic changes nor the changes in the relative frequencies of the gene arrangements through which both species have passed between 1945 and 1951 (see above).

A word of warning must be added at this point. The relative frequencies of the species in collections depends not only upon their incidence in the locality but also on collecting techniques. Thus, *D. persimilis* is more common among the flies collected in the morning than in the evening (Dobzhansky, 1951), *D. azteca* is less frequent when cups with rather fresh fermenting banana bait are used for traps than when large cans with old bait are used (the "Texas method"). Furthermore, there occur local concentrations of these species in various microenvironments. Tables 6 and 7 include, therefore, only the samples collected with the aid of the same technique (banana cups, evening collecting), and in exactly the same neighborhoods.

DISCUSSION

The concept of "type" is inherited from the pre-evolutionary age. Nevertheless, it still colors the thinking of many biologists. It is frequently assumed that natural populations consist of "normal," or "typical," representatives of their species and races, with a scattering of rare "aberrant," or "mutant," individuals. Only where a species is obviously composed of two or more clearly distinct categories of individuals, the existence of polymorphism is recognized as a more or less exceptional situation. Now, in biology the idea of "type" is an oversimplification which is often quite misleading. Careful study discloses that polymorphism is a rule rather than an exception. Mendelian populations, i.e., communities of sexually reproducing and cross-fertilizing organisms integrated by bonds of mating and parentage, are always genetically polymorphic. Of course, the polymorphism is more abundant in some and more limited in other populations. This is because polymorphism is usually, although not necessarily, adaptive. Mendelian populations are poly-

morphic, because every species lives not in a single absolutely constant environment, but in a variety of environments which undergo frequent changes. The greater the diversity of environments to which a population is exposed, the greater, in general, will be the polymorphism. This is because no single genetic constitution is likely to prove superior in adaptive value to all others in all environments. It is manifestly advantageous to a species to include a variety of genetic constitutions which engender optimal phenotypes in different environments that the species is likely to encounter. By and large, the more polymorphic a species is, the greater variety of habitats it can settle and exploit (da Cunha, Burla, Dobzhansky, 1950).

When a species, or any constituent Mendelian population, is exposed to a succession of different environments, it may react to them by genetic reconstructions. The speed of the reaction will depend, among other things, upon the speed of reproduction. Species which give a single generation per year, or in which a generation takes several years, are likely to react to climatic changes which continue for several or for many years. Only exceptionally will such species evince genetic changes in response to seasonal alternations in the environment (as found by Gershenson, 1945, in the hamster). More rapidly breeding organisms may undergo cyclic genetic changes induced by the succession of the seasons, as well as by climatic and biotic variations on successive years. This is the case in *Adalia* (Timofeeff-Rossovsky, 1940) and in *Drosophila*.

Fisher and Ford (1947) discovered changes from year to year in the composition of a certain population of *Panaxia dominula* in England. These changes are presumably due to natural selection. Fisher and Ford allege that this fact invalidates Sewall Wright's theory of genetic drift. What this and similar facts invalidate is the notion that genetic drift is the *sole* cause of evolutionary changes, which Fisher and Ford see fit to impute to Wright. But Wright (1948 and earlier work) has stated quite explicitly that the importance of genetic drift in evolution lies precisely in its interaction with natural selection. The incidence of a genetic variant in a population may vary at times chiefly owing to selection and at other times due chiefly to drift. Genetic variants which differ in adaptive values as much as do the chromosomal forms in *Drosophila* will seldom or never be influenced by drift. Other genetic variants in the same species, such as the heterozygotes for concealed recessive mutant genes, may well be influenced by the drift more than by selection (Dobzhansky and Wright, 1947). Evolution is not caused by any single factor; it is brought about by interaction of many factors, frequently opposed to each other. It is the balance of all the factors which determines the ebb and flow of evolutionary change.

Acknowledgments

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Summary

The sibling species, *Drosophila pseudoobscura* and *Drosophila persimilis*, both show chromosomal polymorphism in the populations of the Yosemite National Park region of the Sierra Nevada of California. Seven gene arrangements are recorded in the third chromosome of the former, and six in the latter species.

In *D. pseudoobscura* the relative frequencies of the ST and AR chromosomes show seasonal changes: ST chromosomes become more, and AR become less, common as the season progresses. Other gene arrangements evince no perceptible changes. No significant seasonal changes have been recorded in *D. persimilis*.

The populations of both species have suffered appreciable changes from year to year. In *D. pseudoobscura* the ST chromosomes waned and AR chromosomes waxed in frequencies between 1945 and 1950, but in 1951 the changes have become reversed. The PP gene arrangement was very rare in 1945 and 1946 but became fairly common in 1951. In *D. persimilis*, WH chromosomes waxed and ST and KL waned in frequencies between 1945 and 1950. Here, again, the year 1951 has brought an almost complete reversal.

There was a succession of drought years in 1946–1950, but the winter 1950–1951 had more than the normal amount of precipitation. It is considered probable that the genetic changes observed from year to year were causally related to the drought and to its abatement. However, the drought has not had a clear influence on the relative abundance of the three related species, *Drosophila pseudoobscura*, *D. persimilis*, and *D. azteca*. *D. persimilis* was, for unknown reasons, much less common in 1951 than ever before. *D. azteca* underwent regular seasonal changes in abundance, which were not appreciably different in 1950 and 1951, despite the genetic changes recorded in the other species.

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NOTES AND COMMENTS

SPECIATION IN WESTERN AMPHIBIA [1]

C. M. Bogert

It is difficult to study speciation in several groups of animals because too little is known concerning the taxonomy or the distributions of the vast numbers of species. Students of the Amphibia, however, have not been confronted with many species—there are probably fewer than 2,500. But many salamanders and frogs, not to mention the less well known caecilians of the tropics, are so secretive or so restricted in their ecological requirements that they are difficult to collect. Even though specimens have been accumulating in museums for generations, there are few species for which precise information concerning the distributions or relationships is available. Indeed studies of the species within the boundaries of the United States were scarcely beyond the pigeonholing stage until the last decade. Despite existing collections such conscientious revisors as Hairston and Pope (Evolution, 2: 266–278) and Stebbins 1949 (commented upon by Mayr, Evolution, 3: 383) found it necessary to carry out extensive collecting themselves before they could fill the gaps that still existed in ranges.

This well illustrated and informative account of the 51 species (two of them introduced frogs from the East) inhabiting the United States, Canada, and Alaska west of longitude 102 now paves the way for more detailed studies of the effects of geographical isolation or of similar problems concerned with speciation. As Stebbins points out, "the occurrence of many species in small, weakly connected, or separate populations in suitable areas in otherwise generally unfavorable habitats, provides a favorable situation for the study of environmental effects on the structure and dynamics of populations."

The student of speciation will be particularly pleased to find that maps showing ranges as well as individual collecting stations in the West have been provided for each of the species and subspecies discussed. Several dubious records have been rejected, and when specimens upon which they were based could not be examined they have been questioned. Stebbins says that he has put into the book what he himself wanted to know about our western amphibians, and since there are already sources of general information concerning the group, he has confined himself "to assembling facts on species." These include descriptions of (and keys to) the eggs, larvae, and adults, as well as accounts of feeding habits, behavior and reproduction, Body temperatures of animals in their native habitat have often been recorded, a notable improvement over such statements as "inhabits cool streams," that were useless to anyone wanting precise information.

The experimental embryologist, or for that matter anyone interested in attacking problems concerned with the evolution of behavior, with the effects of environment, or with countless other phenomena profitably studied in the Amphibia, will find a wealth of information at his disposal.

The book is avowedly an assemblage of "facts on species," but it is not a mere compilation from the literature. Published information has not been neglected, of course, but this has been greatly augmented by the work of Stebbins and his students as well as by unpublished data drawn from the notebooks on file at the Museum of Vertebrate Zoology. Critical review of the evidence has often resulted in new interpretations, particularly of the taxonomic status of some of the populations discussed. Even without additional evidence, reappraisal of existing data has permitted Stebbins satisfactorily to dispose of several "species." The toad isolated in Deep Springs Valley in California that was originally described as a full species, *Bufo exsul,* is manifestly derived from the widespread species *Bufo boreas,* to which Stebbins assigns it as a race. Aside from the fact that numerous isolated but less apparently differentiated populations of *boreas* exist around other desert springs in the general region, it is highly improbable that any physiological isolating mechanism exists. The relegation of *exsul* to subspecific status has the additional advantage of indicating the derivation of the population.

The status of another toad, *B. microscaphus californicus,* is less readily established by Stebbins largely because of complexities introduced by a disjunct distribution and the presence in one region of hybrids between it and a sympatric species, *B. woodhousi.* Hybrids in species whose ranges overlap apparently are far from rare among plants, but extremely few cases of hybridization in nature have been authenticated among the amphibians and reptiles. Thus the case reported by Stebbins is of particular interest. The toad in question was originally described as the coastal California race of *B. cognatus,* a species with which it had little in

[1] Amphibians of western North America. By Robert C. Stebbins. University of California Press, Berkeley and Los Angeles, 1951, ix + 539, pls. 1–64. $7.50.

common. Later differences in morphology as well as in the voice were cited along with other evidence and *californicus* was considered a full species. Next it was placed as a subspecies of *compactilis,* a Mexican species, the range of which was believed to extend into Arizona and Utah. A few years later the name *microscaphus* proposed by Cope in 1867 but long buried in synonymies, was revived for the populations in Nevada, Arizona and Utah. However, since intermediates between it and *B. woodhousi* were noted, *microscaphus* was believed to be a race of this species. The population on the opposite side of the desert in California was therefore placed as a subspecies of *woodhousi, B. w. californicus.*

Stebbins has finally indicated what appears to be the correct solution to the problem. Apparently *woodhousi* and *microscaphus* both occur along the tributaries of the Colorado River in the region centering around southwestern Utah. In some peripheral areas only one or the other is present. But where both occur varying percentages of the population are intermediate. These intermediates are, therefore, construed as hybrids between *microscaphus* and *woodhousi,* rather than as intergrades between subspecies. Since the population on the western side of the desert is so similar in morphology, both as a tadpole and as an adult, it is placed as *B. microscaphus californicus,* the fifth combination in names thus far used to designate it.

Stebbins' conclusions with reference to this species of *Bufo* are similar to those of Blair (1941, Genetics, **26**: 398–467), who studied four species of *Bufo* east of the Rockies and concluded that in "most of the places" where two or more of these species (*americanus, terrestris, fowleri* and *woodhousi*) occur intermediates are also found. Despite the use of such terms as "closed systems" and definitions of species as being populations that are "reproductively isolated," when such evidence of interbreeding occurs between populations that retain their individuality, most modern systematists have referred to the intermediates as hybrids between species. As Simpson (Evolution, **5**: 289) has recently noted, interbreeding may occur between adjacent populations that most modern systematists would call species. However, it is not always easy to determine whether the intermediates are interspecific hybrids or intergrades between subspecies. Netting and Goin (Copeia, 1946, 107) presume that the intermediates between *Bufo terrestris* and *B. americanus* are intergrades, but they do not say whether toads identifiable as *terrestris* and *americanus* occur in the same localities as the supposed intergrades. Without such evidence their arguments are not convincing. Stebbins is on better grounds since he shows that hybrids occur only where both parental species are represented.

Blair suggests that such phenomena do not have much bearing on the origin of new species, but since the hybrids are known to be fertile they point to the "fusion and disintegration of old ones." However, neither he nor others have been able to detect the presence of any isolating mechanism that would account for the maintenance of the individuality in the overlapping species. Blair suggests that several isolating mechanisms working in combination may prevent any mass hybridization and that the breaking down of barriers between the species involved may be of relatively recent origin, possibly coupled with postglacial climatic changes and the activities of man. The changes wrought through human agency in portions of the range of *B. microscaphus* seem hardly sufficient to account for the hybridization in this instance.

Stebbins' useful maps bring to light numerous examples of disjunct distribution of closely related populations. Depending upon the evidence available these populations are interpreted as representing distinct species, recognizable subspecies, or as identical subspecies. More detailed studies may alter some of the conclusions reached, but even an extensive knowledge of the breeding habits, life histories, or ecological requirements rarely enables the systematist to be dogmatic in deciding whether geographically isolated populations would freely interbreed were they sympatric. Breeding experiments may disclose the existence of physiological isolating mechanisms, or even behavioral patterns that point to reproductive isolation. However, until such data are available the systematist relies largely upon such inferences as he can draw from the degree of morphological divergence of the populations in question. Stebbins, unlike many authors of handbooks, presents the evidence upon which he rejects views of others or reaches his own conclusions. These are often tentative, but generally sound.

Included in the present work is a summary of an investigation of the polytypic species *Ensatina eschscholtzi* first published by Stebbins in 1949 when he demonstrated the existence of two series of races separated by the San Joaquin Valley in central California, with an overlap in the ranges of the terminal races in southern California where interbreeding between the two is unknown. It is of interest to note that a similar but not identical distributional picture is now emerging for other species, notably the races of *Rana boylii.* In this species the nominate race is a lowland form with a range that nearly encircles San Joaquin Valley as well as portions of the Sierras; at higher elevations in the Sierras it is replaced by the subspecies *sierrae.* However, *boylii* reappears in a single

colony south of its main range on one mountain within the territory occupied by a third race, *muscosa*.

A similar but considerably more restricted distribution of the three species of salamander now comprising the genus *Batrachoseps* suggests that they are all descended from a single polytypic species that once had a distribution similar to that of *Ensatina*. It is not difficult to account for the existence of two species with overlapping ranges in southern California if it be assumed that these populations represent vestiges of what was formerly a circular overlap like that of *Ensatina* but with one link in the chain now missing. The existence of the third species of *Batrachoseps* in an isolated range in northwestern Oregon offers further support for the belief that the range of an ancestral species that was once widespread has become fragmented, presumably as a result of climatic changes. It has been difficult to account for the coexistence of two closely related species in many areas, but such distributional patterns as those exemplified in these three groups of amphibians provide a sound basis upon which theoretical explanations can be offered. Thus far the evidence accumulating is in favor of the belief that geographic isolation usually precedes reproductive isolation. The phenomena observable in "circular overlaps" do not belie this assumption even though it is plain that reproductive isolation may not be complete until some link in the chain is broken.

Many gaps in ranges will undoubtedly be closed by more intensive collecting in the critical regions. Nevertheless the maps provided by Stebbins are more detailed than any previously available, and they are of particular interest in that clues can often be obtained concerning origins and dispersals by studying the distributions of related species. The distributions of frogs and salamanders are probably more rigorously restricted than those of other terrestrial vertebrates by the moisture requirements of these animals. It is perhaps noteworthy, therefore, that few of the distributional patterns bear any resemblance to "biotic provinces" as mapped by various authors. On the other hand there are some correlations of distributions with the natural vegetation, a map of which is included.

Stebbins' book will serve many purposes and while much remains to be learned concerning western Amphibia, it is plain that the descriptive phase of the work is now being supplanted by studies that have considerably more interest to students of evolution.

EVOLUTIONARY GENETICS

G. G. Simpson

Every reader of Evolution is certainly acquainted with earlier editions of Dobzhansky's "Genetics and the Origin of Species."[1] The first (1937) and second (1941) editions were widely and enthusiastically reviewed. This work is now generally recognized as one of the most important books ever written, either on genetics or on evolution. High evaluation depends not only on the brilliance and originality of the publication. It results even more from the profound and constantly increasing influence of Professor Dobzhansky's masterpiece during the fifteen years since its first appearance. Under these circumstances, the reviewer's task might be confined to announcement that a completely rewritten third edition has now been published. Students of evolution are familiar with the themes treated and the importance of the book. They certainly need no review to convince them that they must study this new edition. Some comparisons with previous editions may nevertheless be of interest.

From the start, "Genetics and the Origin of Species" both marked and developed a new trend in genetical research and theory. This was a movement beyond classical, formal, or what many of us would (but Dobzhansky does not) call Mendelian genetics. The factors of the "genetics of the transmission of hereditary materials" were taken as given. Attention was directed to the play of those factors in *populations*, the field of population genetics, and through *time*, the field of evolutionary genetics. Both these subjects had, of course, been studied previously. They had not been welded into a consistent and integral branch of science, and that was perhaps the major contribution of the first edition of this book.

The processes of evolutionary population genetics are seen as occurring at three levels: (1) origin of raw materials by mutations of genes and chromosomes, (2) changes in populations by changes in frequencies and combinations of mutations, and (3) fixation of such changes by reproductive isolation. Each level has its special basis in underlying factors derived from less evolutionary genetics: (1) in the frequencies and natures of mutations, (2) in the formal laws of transmission, and (3) in (especially)

[1] Dobzhansky, Theodosius. 1951. Genetics and the origin of species. 3rd edition. Pp. i–x, 1–364; 23 text figs.; 15 tables. Columbia University Press, New York. $5.00.

the mechanisms of hybrid sterility. The underlying factors of the second level were already taken for granted in the first edition. Those underlying the first and third levels were not. In the second edition, four chapters, more than two-fifths of the book, had mutation (of both genes and chromosomes) as the line of approach.

The trend toward an autonomous evolutionary genetics that is not so much derived from as it is based on other genetical findings is accentuated by the new treatment of the materials of those four chapters. None of the chapters is retained in the third edition in title or outline. Chromosomal changes (the subject of the longest chapter in the second edition) and polyploidy (also then the subject of a separate chapter) are now reviewed more succinctly and are approached from the viewpoint of evolution, rather than the other way around. Part of this and much other material is now treated in new chapters on adaptive polymorphism and on race formation (now the longest chapter). A significant shift in viewpoint is evident.

The shift is less evident in the new treatment of hybrid sterility. This too is an aspect of formal genetics, fundamentally important as a mechanism that becomes involved in evolution, but distinct from the actually evolutionary processes leading to reproductive isolation. The latter processes are brilliantly discussed in the preceding chapter, but hybrid sterility still has its own chapter in which the approach is less primarily evolutionary. This chapter, too, is entirely reorganized and rewritten. For instance, it now includes material formerly discussed under "chromosomal changes." It is, however, interesting that this chapter seems to have less wholly new material than any other part of the new edition.

It should be emphasized that the revision as a whole does include a very large amount of new material. This goes far beyond bringing each topic up to date and citing more recent literature. Much of the third edition could well be considered a new work on the same subject rather than a revision in the usual sense. In exemplification of this fact, mention may be made of the new chapter on adaptive polymorphism. This reflects Dobzhansky's own major research interest since the second edition, and it includes unusually conclusive, quantitative evidence of effective natural selection in free and laboratory populations. An example on a smaller scale is the excellent, brief account of mutation and selection in microorganisms. *All* the work here reviewed has been published since the second edition of "Genetics and the Origin of Species."

Both in his research and in this book Dobzhansky is characterized by a knack for turning attention to new problems, keeping in the vanguard of what is currently crucial. The other aspect of this tendency is elimination of discussion of what is no longer considered crucial. The second edition of "Genetics and the Origin of Species" appeared the year after Goldschmidt's "The Material Basis of Evolution" and devoted considerable space to refutation of that work. This has now been reduced to casual mention that Goldschmidt's theory of saltatory evolution is fatally opposed by the facts. In the first edition Dobzhansky proposed to give Lamarckian (i.e., neo-Lamarckian) doctrines brief mention, confined to dogmatic rejection. He has clung to this attitude even in the face of the recrudescence of Michurinism under Lysenko, not so much as mentioned in the new edition. There may be some difference of opinion as to whether either of these issues, saltatory evolution and Michurinism, is entirely settled.

The reviewer is too enthusiastic about this book to want to quibble over details. Just to show that nothing is perfect, he might mention that Rensch's "anagenesis" is misspelled both in text and index, that there are many (but decreasing) systematists who still insist on a morphological species concept (contrary to a statement on p. 263), and that the final footnote of the book, which implies that a "Mendelian population" (a term that the reviewer dislikes, by the way) must be homozygous for definitive genes, is oddly at variance with previous discussion.

Finally, note should be taken of the extraordinary fact that this third edition, brought completely up to date, is shorter than the second.

AN ELEMENTARY TEXT ON EVOLUTION[1]

RICHARD LEWONTIN

There has been a great need for a textbook which would present to the elementary student the recent evidence bearing on evolution from genetics and other biological disciplines. Especially needed has been a discussion on an elementary level of the synthesis of these disciplines in modern evolutionary theory. On the whole, Dodson has succeeded in filling this need in the textbook literature. Unfortunately, the

[1] Dodson, Edward O. A textbook of evolution. W. B. Saunders Co., Philadelphia and London, 1952, xviii + 419 + figs. 1–101. Price $5.00.

difficulties of presenting the material to untrained students, as well as an apparent bias on the part of the author, have prevented the book from being entirely satisfactory.

The presentation is divided logically into two sections. The first of these deals with a proof that evolution has, in fact, taken place. This entails a general review of plant and animal phylogeny and distribution. Although relying heavily on recent rather than fossil forms, the evidence is convincingly presented.

The second section of the book, comprising only about one third of the whole, deals with modern theories of the evolutionary process. It is here that some serious objections arise. Dodson divides evolutionary theorists into two schools: that of the Neo-Darwinists and that of Goldschmidt. While ostensibly making no special case for either opinion, Dodson is clearly oriented toward the latter. Thus, the facts which seem to be unsatisfactorily explained by Neo-Darwinism are presented as evidence in favor of Goldschmidt's thesis, while the difficulties entailed in the latter theory, and there are many, are not discussed. The importance of chromosomal abberation both in providing genetic variability and in serving as a mechanism for speciation is given considerable weight. The importance of genic variability in these processes is, on the other hand, underemphasized. The evolutionary roles of concealed genic variability and of adaptive polymorphism are not discussed, despite the abundant evidence available on these points.

While it is highly desirable to discuss all points of view in a science whose theoretical aspects are as yet in a state of flux, it is important to do so without bias, for the powers of discrimination of elementary students are often not sufficient for critical examination.

COMMENTS ON EVOLUTIONARY LITERATURE

ERNST MAYR

Drosophila and evolution.[1] The publication of a new "Texas Bulletin" containing papers by J. T. Patterson and co-workers on *Drosophila* genetics is always an event. The present issue again offers much of great interest, in particular, a penetrating analysis of the *D. virilis* species group. The complex is represented in Europe by *D. littoralis*, which has a certain amount of fertility with *virilis* and with species of the *montana* group. The main barrier to cross fertility between *littoralis* and other members of the virilis group is sexual isolation. Two additional sibling species of the *montana* complex are described by Patterson. They had been in the Texas laboratory for some time, though their specific distinctness was recognized only recently. Not all crosses of these species with other members of the *virilis* group produce hybrids, and all male hybrids are sterile. However, hybrids between *montana* and *flavomontana* are occasionally found in nature, one of the rare cases of natural hybridization in *Drosophila*.

The *virilis* group consists of eight to ten known species and the occasional hybrids can be used for an analysis of chromosomal homology. A stock of *D. virilis* was used as standard strain and the gene arrangements of the other species were determined by crossing with this standard strain. As a result Hsu, who undertook the cytological analysis, established a cytological "phylogeny" of the members of the species group. Three branches arose from the postulated ancestor, the *americana* branch, the European *littoralis* branch, and the *montana* branch. The analysis, which is similar to that of Dobzhansky and collaborators for the *D. pseudoobscura* group, can establish the sequence of relationship rather unequivocally. What is, of course, always difficult to determine is which of two gene arrangements is more primitive. Much new material is presented in support of Patterson's hypothesis of a hybrid origin for *D. americana* (as the result of a cross between *novamexicana* and *texana*). Actually, the new facts would seem to make an alternative explanation by far more plausible. *D. americana* is a widespread species with considerable geographical variability of its genetic contents and gene arrangements. Many eastern populations differ quite strikingly from western ones. It would seem probable that some peripheral populations in the west with a depleted store of inversions became isolated and evolved into *novamexicana*, while correspondingly an isolated population in the southeast evolved into *texana*. The high fertility between *novamexicana* and Nebraska *americana* is additional evidence. In fact, it would seem possible to consider *novamexicana* only subspecifically different from *americana*. This interpretation raises certain difficulties with respect to the metaphase chromosomes of *novamexicana*, which, however, appear not insurmountable. *D. americana* with about 13 known gene arrangements, which are

[1] Patterson, J. T., *et al.* 1952. Studies in the genetics of *Drosophila*. VII. Further articles on genetics, cytology, and taxonomy. Univ. Texas Publ., no. 5204, 251 pp.

unequally distributed geographically, would seem well qualified to throw off peripherally populations with a depleted store of variability. Now that it is established (through the work of Dobzhansky, Dubinin, and others) that different gene arrangements are associated with genes of different viabilities, geographical variation in the presence and frequency of inversions is no longer surprising. Whatever the final interpretation of the phylogeny in the *americana* group is, it is undoubtedly a fascinating problem of evolution.

In all, there are 13 contributions to this volume dealing with various aspects of *Drosophila* genetics and evolution, with particular emphasis on wild species. The Mexican and Brazilian subspecies of *D. fulvimacula* differ not only in the color pattern of the mesonotum but also by partial reproductive isolation. Although 98 per cent of hybrid males had motile sperm, only 48 per cent of the F_1 females and only 22.5 per cent of the F_2 females were inseminated. Additional evidence indicates at least two isolating mechanisms, sexual isolation between unlike males and females, and inability of the sperm to fertilize the eggs in the receptacles of the females. This is another instructive example of geographical variation of isolating mechanisms.

D. melanica is added to the species with great variability of gene sequence in a single chromosome (21 sequences in chromosome 2). A phylogeny of the gene sequences was formulated and mapped. Only 4 of the gene sequences were found in the desert populations of this species.

In view of the great general interest in *Drosophila*, a revision of the Nearctic genera of Drosophilidae (excluding *Drosophila*) by M. R. Wheeler should prove very useful. He recognizes 72 species in 20 genera. Keys are given. The genera are unfortunately treated in alphabetical sequence so that closely related genera and even probable synonyms, like *Sinophthalmus* (p. 208) and *Phortica* (p. 168) are widely separated from each other.

Polymorphism and population structure.[2] Further studies of the interesting polymorphic population of the moth *Panaxia dominula* near Oxford (see Evolution, **2**: 279–294, 1948). Two new populations were found about one mile away, but extensive marking failed to reveal interchange of individuals; gene flow must be slight. Eggs are deposited by the females during a period of more than 8 days while the female continues to change her location. This leads toward panmixia within each colony. The observed frequency of the *medionigra* gene in the Cothill population between 1939 and 1950 indicates that there is no conspicuous change of its selective value from year to year, although there is the possibility of a correlation of the selective advantage of this gene (in 6 of 8 years!) with the rate of change in population size. There has been a steady decline in the frequency of the *medionigra* gene from 1939 to 1950, but the reasons for the deviations from the expected value are not explained. If the selective disadvantage of the heterozygotes is assumed to be constant, it can be calculated as being about 10 per cent. The *medionigra* gene is not observed in the two other populations. Females live longer than males but mate only once. Males are capable of copulating successfully with a larger number of females. At the beginning of the breeding season there are more males than females; at the end of the season the ratio is reversed. This system achieves the rapid fertilization of every freshly-hatched female. The continued study of this population promises to shed much light on the interaction of genetic factors, environment, and population structure.

Selective equilibrium.[3] A sample of 189 chickens was tested for three characters: number of eggs laid, number of chicks hatched, percentage of chicks hatched, all three characters being of obvious selective significance. When the birds were grouped according to the weight of their eggs it was found that the maximum values for all three viability characters were found among the producers of medium-sized eggs. The artificial selection for large egg size is thus, to some extent, counteracted by natural selection in favor of genes which are associated with medium egg size. This work furnishes additional experimental evidence for the strength of the factors which prevent or delay the full success of selection, even powerful selection, on a single character.

Endosymbiosis and evolution.[4] The study of symbiotic microorganisms, particularly advanced by Buchner and his students, has led to contact with many branches of biology. The field has also revealed much of interest to the evolutionist. Some of these symbioses must be very old. For instance, the Blattidae (cockroaches) and the primitive termites, their nearest relatives, are characterized by the same highly specific bacterial symbiosis. It is evident

[2] Sheppard, P. M. 1951. A quantitative study of two populations of the moth *Panaxia dominula* (L.) Heredity, **5**: 349–378.

[3] Lerner, I. Michael. 1951. Natural selection and egg size in poultry. Amer. Nat., **85**: 365–372.

[4] Buchner, P. 1951. Symbiose-Forschung und Stammesgeschichte. Die Umschau, **8**: 225–227.

that it must have already existed in their common ancestors in the Paleozoic. Symbioses in many insect groups that feed on plant juices (Peloriidae, Aleurodidae, Psyllidae, Aphids) are uniform and universal within each group. They also must be ancient. In other groups, such as the hemiptera and anopleura, there is great variability in the structure of the organs that house the symbionts and in the methods of transmittal. Even related genera may differ fundamentally. In these cases there is overwhelming evidence in favor of repeated, independent acquisition of symbiosis. In groups with several symbionts, the sequence of invasion can usually be established without difficulty.

Time and evolution.[5] One of the most important results of biological, and particularly paleontological, research is that "biological time" is not constant. Rate of evolutionary change, as well as rate of speciation (origin of discontinuities), depends on so many intrinsic and extrinsic factors as to make them an uncertain foundation of time scales. The causes for this difference in rates are still disputed. Rapid, as well as slow, rates are found in land, freshwater, and marine animals, although on the average land animals speciate more rapidly than marine animals. The rate of phyletic change is largely independent of the length of each generation, as Simpson and Zeuner have pointed out. The thesis that periods of climatic change or geotectonic upheavals are times of rapid evolution is very popular, but the evidence is rather ambiguous.

Schindewolf presents a wealth of material, in part based on the prior studies of Rensch, Simpson, and Zeuner, dealing with the problem of rates and particularly with its yet unsolved aspects. The average life span of genera of ostracods, gastropods, bryozoa, brachiopods, and foraminifera is 50 to 90 million years. In some phyla the life span was larger in the Paleozoic than in the more recent strata; in others the reverse is true. Only the ammonites, with an average life span of 1 to 3 million years, differ drastically from nearly all other invertebrates. Should this reflect excessive splitting by taxonomists induced by a wealth of external characters?

More important is the fact, stressed by Rensch, Simpson, Cloud, Schindewolf, and many other paleontologists, that there is often an almost explosive rate of evolutionary change at the beginning of a new taxonomic "type" to be followed by a period of slow evolution or virtual stagnation. Schindewolf used to cite these phenomena as proof for macromutations. In the present publication he minimizes genetic interpretation and concentrates on a presentation of the puzzling facts. It is evident that a satisfactory explanation has not yet been presented. A mere shift into a new ecological niche is not a sufficient explanation: The bats have entered many new niches and have speciated very actively throughout the Tertiary, but have not changed their basic type in the last 50 million years. Similar statements can be made for the birds, turtles, crocodilians, the insects, and many other groups.

Paleontologists of past generations have tried to interpret these findings as a refutation of the findings of genetics. Actually, there is nothing in modern genetics which is in the slightest contradicted by these findings of paleontology. Yet, there is much in the findings of paleontology for which a genetic interpretation has not yet been found. Experimental genetics until recently has been essentially single-locus-genetics. The student of phylogenies, however, deals with integrated gene complexes. There is much known which indicates that there are very well integrated and hence exceedingly conservative gene complexes, and others that are less well integrated and hence more labile. Periods of rapid evolutionary change may well be periods during which the gene complex is unbalanced after having entered an entirely new adaptive zone or (what is actually only a special case) after having made a biochemical invention of major selective significance. As soon as such a gene complex has become re-integrated, it will be selected for stability (as Schmalhausen and Heuts have emphasized) and evolutionary progress will slow down to a walk. Such a process would fit the paleontological facts as well as the established genetic theory. It seems to me that it would be far better to interpret puzzling paleontological phenomena by broadening the well substantiated current genetic concepts rather than trying to replace them by new genetic theories which are contradicted by many of the facts of population and physiological genetics.

Species and speciation in coregonids.[6] Since coregonids are important food fishes, much has been written on their systematics, perhaps more than on any other kinds of fishes, except the herring. Nevertheless, we seem further from agreement on their classification than ever. Steinmann's detailed monograph of the Swiss coregonids is therefore most welcome, presenting, as it does, a wealth of new data. Where Steinmann is critical of previous work, such as of the rigid system of four species in central

[5] Schindewolf, Otto H. 1950. Der Zeitfaktor in Geologie und Paläontologie. Schweizerbart, Stuttgart, 114 pp.

[6] Steinmann, P. 1950–1951. Monographie der schweizerischen Koregonen. Schweiz. Zeitschr. Hydrologie, **12**: 109–189, 340–491; **13**: 54–191.

Europe and of the use of growth rate as chief taxonomic criterion, he is convincing. He seems less successful where he tries to give new interpretations. Perhaps no solution is possible of the problem of coregonid classification since there has been much introduction of fry from one lake into another, as well as considerable changes in the water conditions of some lakes. However, before undertaking any further speculations on the number and relationship of the species, one should first make a proper statistical analysis. An application of discriminate functions and of other modern methods might help to place into a definite category many of the specimens which superficially appear intermediate.

Steinmann's solution to consider all Swiss coregonids as a single species, the populations of each lake as various ecotypes of a single subspecies ("natio") is evidently not a realistic presentation of the facts. Some of these populations (within a lake) are reproductively isolated either because they have different breeding seasons or by other mechanisms (some are polyploids according to Kupka). There is much to indicate that the multiple colonization theory is correct, however, in a less rigid manner than maintained by Wagler. It is possible and even probable that the same river species (or migratory species) has invaded a given lake repeatedly and that it depends on the ecological properties of the earlier colonists which niche the later colonists can occupy. It is therefore probable that the pelagic forms of lakes are not necessarily more closely related to each other than they are to the benthonic forms nor the shore and the bottom forms among themselves. That much, however, seems certain that the often very distinct populations which co-exist in the same lake cannot possibly be ecotypes. Attacking the *Coregonus* problem with new methods (controlled transplantation, as done by Svärdson), an analysis of the population samples with more powerful statistical methods, further cytological and serological work, might yet lead to a solution of the now hopeless-appearing problem.

A study of the piñon mouse.[7] This detailed analysis of individual and geographic variation in a single species is another manifestation of the trend toward intensive studies in the taxonomically better known groups of animals. *P. truei* is a member of one of the eight species groups in the subgenus *Peromyscus*. The four species of this group are restricted to the western United States and Mexico, with three of the species being more or less peripheral to the widespread ***truei***, but with partially overlapping ranges. Within *P. truei* twelve subspecies are recognized, belonging to two groups east and west of the Sierra Nevada which are barely in contact with each other at one or two places. Within each subspecies group there are clinal changes of size and proportions, and a general resemblance between the color of the pelage and the color of the substrate. The population at the tip of Lower California resembles very closely that across the bay in Sonora. This is ascribed to parallelism. There are various parallelisms between kind of vegetative cover on one hand and various morphological traits, such as size of ears and feet, length of tail and general coloration. Descriptive accounts of individual species, such as presented in this report, are a necessary basis for comparative studies, of which we are now badly in need.

Geographic variation in the Lepidoptera.[8] After an introduction by C. L. Remington on the principles of geographic variation, Margaret M. Cary discusses subspeciation among the sphingid moths of the West Indies; A. B. Klots presents cases of speciation and subspeciation of Holarctic butterflies in North America (with particular attention to *Colias* and *Boloria*); and B. P. Beirne treats subspeciation in European Lepidoptera. Eugene Munroe points out that in the microlepidoptera, in contradistinction to the macrolepidoptera, the most nearly related species is usually sympatric, but on a different food plant. There is little evidence of geographic variation, and the door should be left open for possible mechanisms of sympatric speciation. L. P. Grey discusses the striking geographic variation of *Speyeria atlantis*, which has many more or less isolated populations in the western mountains that appear to be on the borderline of specific distinctness. The full story of the complex history of this species and its close relatives has not yet been written.

Sibling species or subspecies?[9] With the common Japanese frog *Rana nigromaculata* another rather similar frog is found which was described by Ito in 1941 as a new subspecies (*brevipoda*). The data given by Moriya show clearly that two sibling species are involved. They are sympatric but differ in ecology, call notes, and general behavior. Fertile hybrids

[7] Hoffmeister, Donald F. 1951. A taxonomic and evolutionary study of the Piñon Mouse, *Peromyscus truei*. Illinois Biol. Monogr., **21** (4): 104 pp., 24 figs., 5 pls. $2.50 (paper), $3.50 (cloth).

[8] Remington, Charles L., *et al.* 1951. Symposium: Geographic subspeciation in the Lepidoptera. The Lepidopterists' News, **5**: 17–35.

[9] Moriya, K. 1951. On isolating mechanisms between the two subspecies of the pond frog, *Rana nigromaculata*. Jour. Sci. Hiroshima Univ., B, **12**: 47–56.

can be produced in the laboratory, but are never found in nature.

Sibling species.[10] Ramme gives a short history of this concept. It was first introduced into the literature by Pryer (1886, Opalocera Nihouiana, Yokohama, p. 2) as "dual or twin species" and extended by Ramme in 1930 (Mitt. Zool. Mus. Berlin, vol. 16, p. 800) to "Geschwisterarten," to include groups of 3 or 4 exceedingly similar species. Some entomologists thought that sibling species differ in history or biogeography from ordinary species, but Ramme points out correctly that they have the same characteristics as all other species, except morphological similarity. Ecological and other biological analysis invariably reveals differences greater than the morphological ones.

Adaptation in a human race.[11] The Scandinavian Lapps are usually considered mongoloids or at least strongly mixed with mongoloids. However, they differ conspicuously from mongols in their blood groups, facial height, and other characters. The author believes that the Lapps are an old European population, not at all related to the mongols, which has become adapted to life in the arctic and subarctic zones of northern Europe and have there acquired various similarities to the mongoloid groups that live in similar environments in central and northern Asia.

[10] Ramme, W. 1951. Zur Systematik, Faunistik und Biologie der Orthopteren von Südost-Europa und Vorderasien. Mitt. Zool. Mus. Berlin, **27**: 313–323.

[11] Lundman, B. 1952. Ergebnisse der anthropologischen Lappenforschung. Anthropos, **47**: 119–132.